ASPECTS OF THE BIOLOGY OF *ASTROSTOLE SCABRA* (HUTTON, 1872)

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ABSTRACT

The known geographical distributions of the genus *Astrostole* and the New Zealand species *A. scabra* are modified extensively by new records presented here. The supposed dispersal agency, West Wind Drift, is shown to have been incapable of producing the present pattern, and interaction between a west to east current north of the sub-tropical convergence, an eastern Pacific surface gyre and the Peru Coastal Current is suggested as the dispersal mechanism.

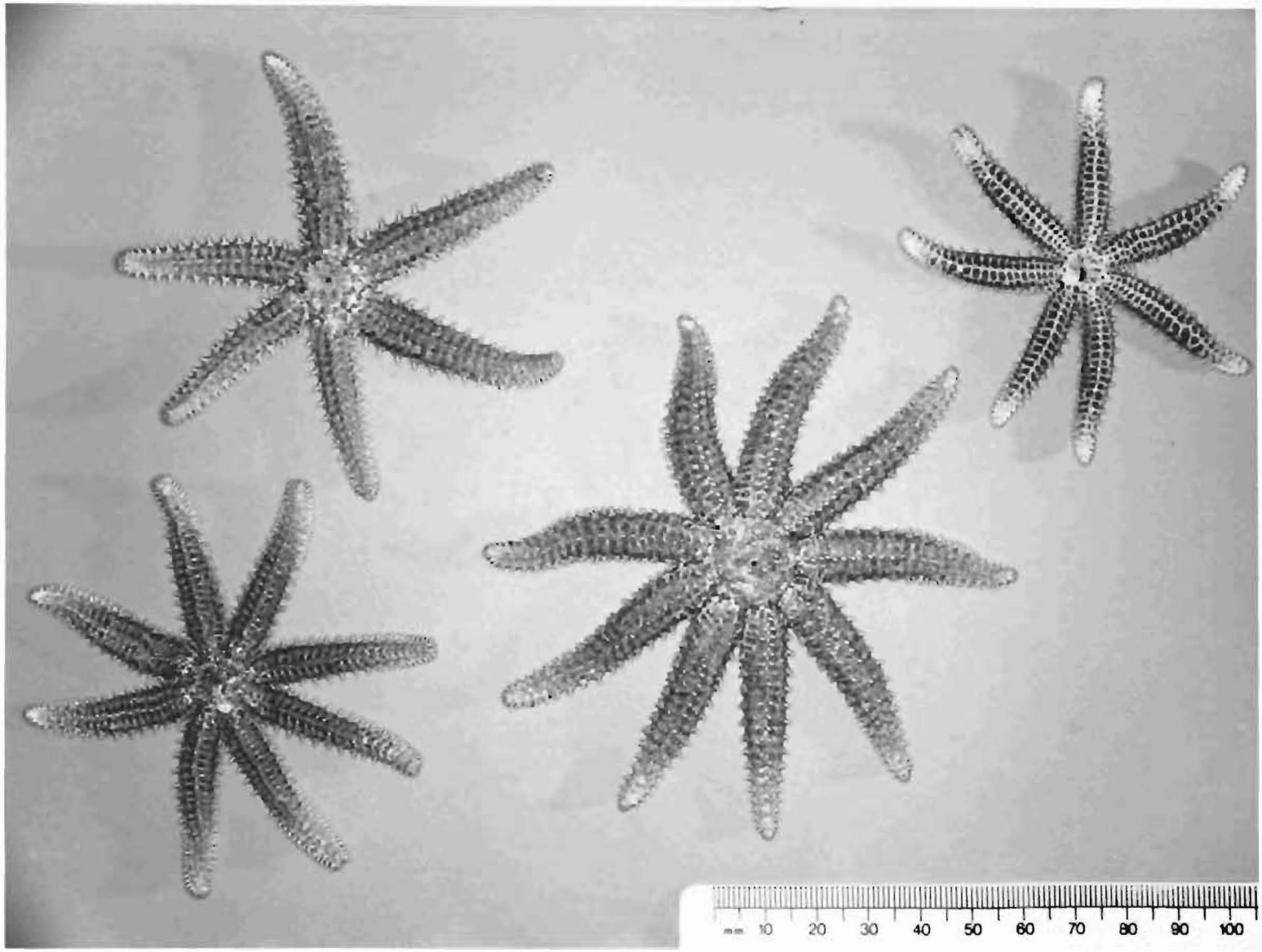
Studies conducted at Kaikoura (42^{o},25'S, 173^{o},42'E) showed that intertidal *A. scabra* were not site specific, and were heavier, smaller, immature, and regenerated more rays than subtidal ones. Longevity in *A. scabra* exceeds six years and sexual maturity is achieved during the fourth year of life, after seastars have migrated to depths of 20-146m.

During three years of study, spawning in subtidal *A. scabra* occurred once per year in late August - early September. The volume of gonad produced by individual seastars was reduced by ray damage, and a few, large intertidal seastars developed small gonads.

A. scabra is a food generalist and scavenger with a diet composed chiefly of molluscs and crustaceans belonging to more than sixty genera. The proportion of intertidal *A. scabra* feeding fluctuated seasonally, peaking at 42% in January 1976 and falling to 23.7% in June 1976. In laboratory trials, *A. scabra* could discriminate between prey species and preferentially consumed *Ischnochiton maorianus* (Mollusca: Polyplacophora). Fifteen molluscs and one echinoid exhibited escape reactions to contact with the seastar. Field data indicated that dietary composition altered qualitatively with increased

predator size such that prey was partitioned amongst seastar size classes according to both species and size. Eight of nine major prey species have spatial and size refuges from predation.

FRONTISPIECE: Dried specimens of six, seven, eight and nine rayed *Astrostole scabra*.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INTRODUCTION

New Zealand's asteroid fauna has been studied primarily from a taxonomic standpoint (see review in Clark, 1970), and to provide distributional data in support of theories regarding the origin and migration of Australasian echinoderms (Fell, 1949, 1953a, 1962a). The general biology of New Zealand asteroids has not received much attention although Maxwell (1957) tested the responses of some larval asteroids to manipulated environmental conditions, Crump (1969) studied feeding, growth and reproduction in *Patiriella regularis* and *Coscinasterias calamaria*, and Martin (1970) investigated the feeding biology of six species. More recently, Barker (1977a, 1977b, 1978) examined larval development and recruitment in *Stichaster australis* and *C. calamaria*, and Emson (1978) described the process of fission in *Allostichaster polyplax*. Apart from taxonomic and distributional considerations, the general biology of *Astrostole scabra* was virtually unknown. Bennett (1927), Clark (1958) and Crump (1968) used *A. scabra* in the study of molluscan escape reactions, and Fell (1962b) published some very brief notes on its diet. Recently, Binyon (1976) used *A. scabra* in experiments on podial wall permeability.

A. scabra, a forcipulate asteriid, is New Zealand's largest seastar (Fell, 1959) and can grow to a radius of 365mm (pers. obs.). Abactinal colour is variable and intertidal individuals may be grey, blue, brown, purple, or a mottled mixture of these. Specimens from deeper waters range from dull red, dull orange, blue-pink, pink, pink-white to dark brown. The tube feet of all specimens are always bright orange with the exception of the cream coloured terminal podia. Rays usually number seven, but six, eight, nine and ten-rayed specimens

comprise 2.6% of the population.

This study was conducted from the University of Canterbury's Edward Percival Marine Laboratory, situated at Kaikoura (42°,25'S, 173°,42'E) on the eastern coast of New Zealand's South Island. The aims of the study were to clarify the geographical distribution of each member of the genus *Astrostole*, and to study the agencies by which the observed pattern may have arisen.

There is a paucity of information on the population dynamics of seastars. A study aimed at outlining movement, longevity and age at first maturity in *A. scabra* was therefore undertaken, and the reproductive cycle of the species was determined.

Because of the current interest in the effects of asteroid predation on intertidal prey communities, an intensive investigation of dietary composition in four, geographically separated sub-populations was completed. In order to interpret these data, laboratory and field observations were made on selective feeding, prey escape reactions, and biotic influences on dietary composition.

SECTION 1

CHAPTER 1. DISTRIBUTION AND DISPERSAL OF THE GENUS *ASTROSTOLE* FISHER, 1923 (ECHINODERMATA: ASTEROIDEA)

INTRODUCTION

The six known species of *Astrostole* are confined to, and characteristic of, the South Pacific (Clark, 1946), and are the most numerous Asteriidae of the region (Fell, 1962a).

Fell (1962a) postulated that the dispersal of *Astrostole* species was by means of larval transport, or epiplanktonic drift of adults, in the West Wind Drift. The bases of this hypothesis are that the West Wind Drift existed through much of the Tertiary, and secondly, that the sources of circumpolar genera lie at the western end of their range. Fell (1962a) considered further, that the donor region for easterly species in the genus was New Zealand (including Lord Howe and Norfolk Islands), and that the first recipient outpost was the Kermadec Islands. The same authority (Fell, 1949, 1953a) suggested that the genus *Astrostole* arose, probably, from Indo-west-Pacific stock in the early Pliocene (10m yrs. B.P.), following the extinction of "old Indo-Pacific" stock at the close of the Miocene. This local extinction was probably caused by "catastrophic" climatic cooling which occurred at that time (Fleming, 1975). Although Fleming (1975) considered that it was impossible "to tell whether some colonists came...via the islands and shallows of submarine ridges or via Australia", Fell (1953a) and Pawson (1965) favoured a northern Indo-west-Pacific origin for Tertiary Australasian echinoderm faunas.

DISTRIBUTION OF *ASTROSTOLE*

Astrostole is composed of six species: *Astrostole scabra* (Hutton, 1872), *Astrostole rodolphi* (Perrier, 1875), *Astrostole platei* (Meissner, 1896), *Astrostole paschae* (Clark, 1920), *Astrostole insularis* Clark, 1938, and *Astrostole multispina* Clark, 1950. Fisher (1928) considered the monotypic genus *Meyenaster*, represented by *M. gelatinosus* (Meyen, 1834), to be a derivative of *Astrostole*. In the present work therefore, *M. gelatinosus* is considered an easterly derivative of the Australasian donor stock.

Five of the *Astrostole* species were thought to be restricted to single or small groups of islands in the South Pacific Ocean, south of the Tropic of Capricorn (Madsen, 1956). *A. scabra* occurs in Tasmania (Dartnall, 1969a, 1969b), the Chatham Islands (McKnight, 1967), Long Reef, New South Wales (pers. obs. based on a specimen held in the Australian Museum), and on the New Zealand mainland (see below). *A. insularis*, originally known from Lord Howe Island only (Clark,1938), also occurs at Long Reef, and Port Jackson, New South Wales coast (pers. obs. based on specimens held in the Australian Museum). Similarly, *A. multispina* was thought to be endemic to Norfolk Island (Clark, 1950), but has been collected recently from Long Reef, Port Macquarie, Port Stephens, and Manly, New South Wales (pers. obs. based on specimens held in the Australian Museum and the National Museum of New Zealand). *A. platei* was considered endemic to the Juan Fernandez Islands (Madsen, 1956; Meissner, 1896), but occurs also on the Desventuradas Islands (Codoceo, 1976). Of the others, *A. rodolphi* is restricted to the Kermadec Islands (Perrier, 1875; Sladen, 1889; Pawson, 1961; McKnight, 1968), and *A. paschae* is endemic to Easter Island (Clark, 1920; Devaney, 1972; Codoceo, 1974). *M. gelatinosus* occurs from Iquiqué to Isla san Pedro on the Chilean coast (Dayton *et al.*, 1977; Madsen, 1956;

Prof. P. Sanchez, pers. comm.). Table 1.1 and Figure 1.1 summarise the geographical distribution of the genus.

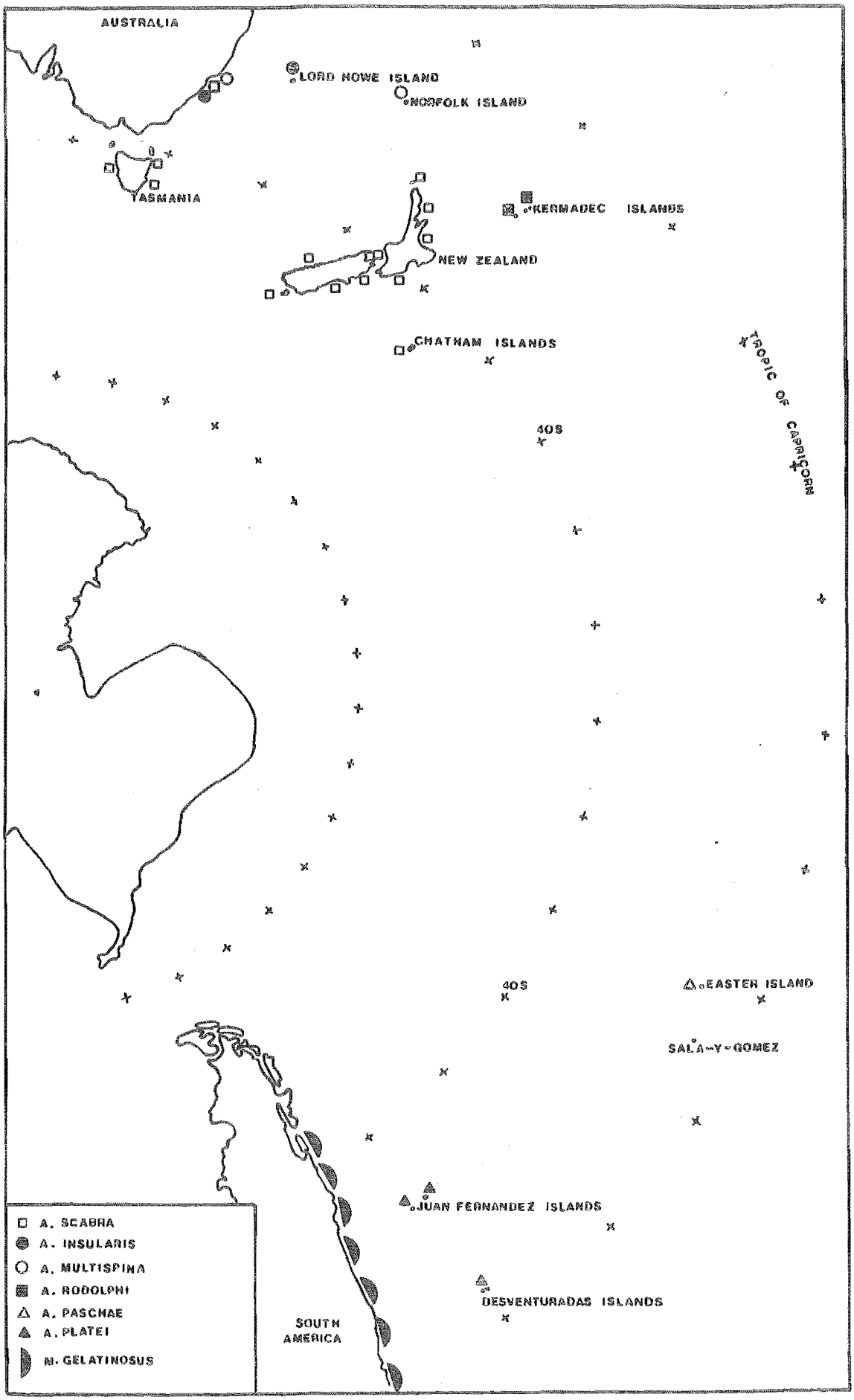
DISTRIBUTION OF *ASTROSTOLE SCABRA*

Hutton (1872), in his original description of *A. scabra*, recorded its distribution as "Pacific Ocean". In a series of papers from 1947 to 1962, Fell gave the distribution of *A. scabra* as the North Island, south of the Auckland Peninsula, and the northern two-thirds of the South Island. Later, its geographical distribution was given as "throughout New Zealand" and then as "the entire New Zealand coast as far south as Otago". Pawson (1961) supported the last view, but later (Pawson, 1965) recorded the distribution as restricted to areas between a point south of East Cape and Banks Peninsula, despite the fact that earlier, Graham (1962) had recorded the species from the North Otago shelf, albeit as rare. Other records (Bennett, 1927; Dix, 1969; Farquhar, 1898; Maxwell, 1957; Mortensen, 1925; Poore, 1969; Ralph and Yaldwyn, 1956) all fall within the limits given by Pawson (1965).

A. scabra was not recorded from the Chatham Islands by Young (1929) or Fell (1960), but a single, large, littoral specimen was collected from this locality by McKnight (1967). A specimen of *A. scabra* collected from "off the Chatham Islands" in 1949 is also deposited in the National Museum of New Zealand. In 1969, *A. scabra* was discovered on the eastern, north-eastern and western coasts of Tasmania (Dartnall, 1969a, 1969b). However, D. Wolfe (pers. comm.) considers *A. scabra* uncommon in Tasmania. A single specimen of *A. scabra* from Long Reef, Sydney, is held in the Australian Museum Collection.

Early accounts regarding the distribution of *A. scabra* in New Zealand waters are consistent in that the species was never recorded from north of East Cape. Pawson (1961), using data from Garner (1959),

FIGURE 1.1: Distribution of *Astrostole* and *Meyenaster* in the South Pacific.


AUSTRALIA
LORD HOWE ISLAND
NORFOLK ISLAND
TASMANIA
KERMADEC ISLANDS
NEW ZEALAND
CHATHAM ISLANDS
TROPIC OF CAPRICORN
40S
40S
EASTER ISLAND
SALA-Y-GOMEZ
JUAN FERNANDEZ ISLANDS
DESVENTURADAS ISLANDS
SOUTH AMERICA
A. SCABRA
A. INSULARIS
A. MULTISPINA
A. RODOLPHI
A. PASCHAE
A. PLATEI
M. GELATINOSUS

suggested that hydrological conditions in the vicinity of East Cape and Cape Egmont formed a barrier restricting the northward migration of southern forms. Clark (1970) correctly doubted the effectiveness of East Cape as a barrier to asteroids, at least to *A. scabra*, as is confirmed by the northern records referred to later.

A. scabra is common at the Snares Islands (Horning, 1977), and this record represents the southernmost, and only subantarctic occurrence of the species. In the Otago district, *A. scabra* is not common intertidally. However, it is quite common sub-tidally near exposed rocky shores in the area close to the entrance to Otago harbour (Prof. J.B. Jillett, pers. comm.). The sole records from the west coast of the South Island are from Daggs Sound and Open Bay Islands, Westland, where it is locally abundant (R.H. Mattlin, pers. comm.). *A. scabra* also occurs at Leigh (Gordon and Ballantine, 1976), and is known from four other points on the east coast of the North Island, north of East Cape, and from Kapiti Island on the west coast of the North Island (pers. obs. based on specimens held in the National Museum of New Zealand). Figure 1.2 summarises the distribution of *A. scabra* in New Zealand waters.

A. scabra is most commonly known from rocky bottoms, although in the Kaikoura region it also occurs sub-tidally on pebbles and on hard clay with high shell debris content. A degree of water turbulence also appears to be a prerequisite for its occurrence. Farquhar (1894) noted, "it loves to be in the wash of the waves, where they break on the exposed parts of the coast". *A. scabra* is not regarded as a member of New Zealand's deep-sea (200m or deeper) echinoderm fauna (Fell, 1953b, 1958). Fell (1949) gave its bathymetric range as 0-50m, and Graham's (1962) records are from 9-55m. Apparently on the basis of the above, Clark (1970) gave its depth range as 0-200m. The deepest record obtained during this study is from Kaikoura and the Snares Islands and

FIGURE 1.2: Distribution records of *Astrostole scabra* in New Zealand.

O——— published previously

●——— new records

1: Three Kings Islands (NMNZ)

2: Leigh (Gordon and Ballantine, 1976)

3: Great Barrier Island (NMNZ)

4: Mayor Island (NMNZ)

5: Lottin Point (NMNZ)

6: Mahia Peninsula (Pawson, 1965)

7: Mataikona (NMNZ)

8: Cape Palliser (NMNZ)

9: Wellington (Mortensen, 1925)

10: Cape Campbell (Bennett, 1927)

11: Kaikoura Peninsula (present study)

12: Lyttelton (Bennett, 1927)

13: Chatham Islands (NMNZ)

14: North Otago Shelf (Graham, 1962)

15: Otago Peninsula (present study)

16: Port Pegasus (NMNZ)

17: Snares Islands (Horning, 1977)

18: Daggs Sound (NZOI)

19: Open Bay Islands (present study)

20: Nelson (Mortensen, 1925)

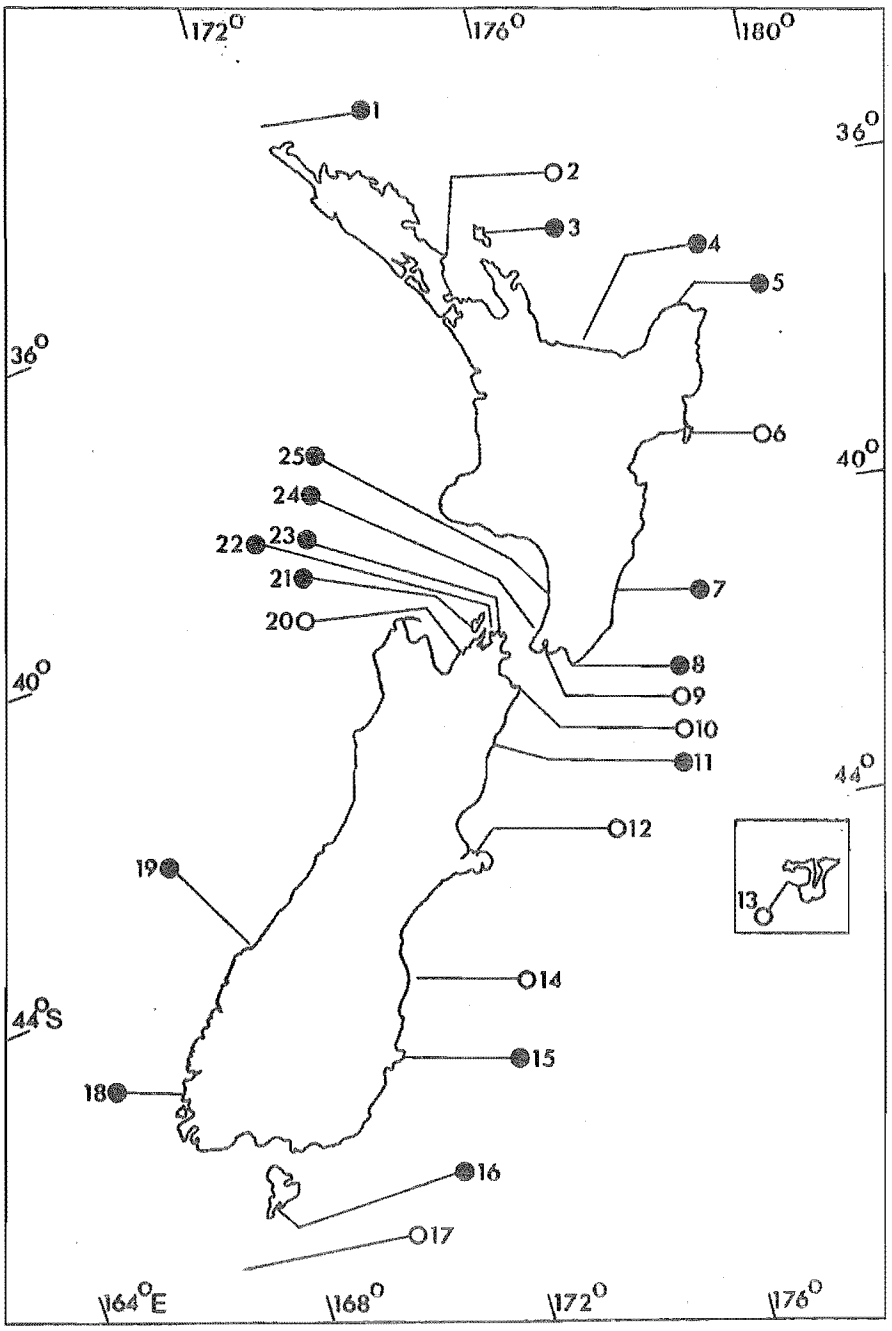
21: D'Urville Island (present study)

22: Cape Jackson (present study)

23: Chetwode Islands (present study)

24: Kapiti Island (NMNZ)

25: Waitarere Beach (NMNZ)


172°
176°
180°
36°
40°
44°
44°S
164°E
168°
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is 146m. Tasmanian records range from 0-30m (D. Wolfe, pers. comm.).

DISCUSSION

Knowledge of the geographical distribution of the genus *Astrostole* has been extensively modified by new records. Only two species, *A. rodolphi* and *A. paschae* are now considered endemic to single island outposts. *A. multispina*, *A. insularis*, *A. scabra* and *A. platei* have less restricted distributions than was supposed hitherto. Of the latter four species, *A. scabra* appears to have shown the most marked extension to its range. The recent appearance of *A. scabra* in Tasmania can be ascribed to one of three reasons. Firstly, the species may have a long history in the area, but may not have been noticed until 1969. Secondly, many New Zealand marine animals, including the asteroid *Patiriella regularis*, are known from the region, and Dartnall (1967) suspected that these may have been introduced in 1930 on the shells of imported oysters, *Ostrea angasi*. *A. scabra* may have been introduced at the same time. Thirdly, *A. scabra* may have been introduced to Tasmania on the fouled hulls of ships.

A. scabra is a large, conspicuous member of the intertidal community and is unlikely to have remained unnoticed had it been present for any length of time. The smallest specimens known from Tasmania have a radius of 100mm (Dartnall, 1969b), therefore the possibility that the species has either a long history, or has been present since at least 1930 must be viewed as unlikely. Pliocene and post-Pliocene echinoderm migrations in Australasia have been essentially from west to east (Fell, 1953b). Man is the only agency regularly opposing this pattern (Dartnall, 1969b), and transport on the fouled hulls of ships has been cited as a means of dispersal in barnacles (Bishop, 1947), and ascidians (Morton and Miller, 1973). Indeed, Hyman (1955) suspected that ships may have been responsible for the introduction of the asteroids

Coscinasterias calamaria to South African waters and *C. tenuispina* to Bermudan and West Indian waters. Although this mechanism may well transport firmly-attached sessile species over great distances, it remains an unattractive hypothesis for the explanation of the distribution of relatively motile, loosely-attached species, such as asteroids. Since no theory is entirely satisfactory, the recent eruption of *A. scabra* in Tasmanian waters must remain enigmatic.

The first record of *A. scabra* from the Chatham Islands is of a single specimen taken in 1949. This species was not recorded as being present by two expeditions (Young, 1929; Fell, 1960), and indeed, McKnight's (1967) record is based on only one specimen. Knox (1954) considered that the intertidal fauna of the islands was derived from New Zealand by way of a tongue of cool subantarctic water deflected from the south-eastern New Zealand mainland. The limited and sporadic occurrence of *A. scabra* at the Chatham Islands may be the result of occasional transport of larvae from the mainland via this current. The shallow Mernoo Bank, on the Chatham Rise, may act as an intermediate "stepping-stone".

A. scabra has a wide distribution in New Zealand waters, and far from being stenotopic as suggested by Fell (1949), the species is eurytopic, and should be regarded as one of the group of echinoderms which occurs along the entire east coast of New Zealand (Pawson, 1965).

A. multispina and *A. insularis* are locally common on rocky intertidal reefs in the mid-N.S.W. area, and it is unlikely that Clark (1946), in his exhaustive work on Australian echinoderms, would have overlooked them. Thus, it seems likely that the occurrence of these three species in the N.S.W. area is of recent origin. All members of the genus appear to be stenobathic (Table 1.1). Lord Howe Island, Norfolk Island and New Zealand are separated from Australia by waters deeper than 1000m (van der Linden, 1970). Available information

TABLE 1.1. The known distribution and bathymetric range of *Astrostole* and *Meyenaster*

Species	Max. radius (mm)	Known bathymetric range (m)	Geographical distribution	Sources
A. scabra	360	0-146	N.Z./Tasmania/ N.S.W./Chatham Islands	Present study, Dartnall, 1969a, b, McKnight, 1967, AM
A. insularis	110	0-60	Lord Howe Is./ N.S.W.	Clark, 1938, AM, NZOI.
A. multispina	100	0-250	Norfolk Is./ N.S.W.	Clark, 1950, AM, NZOI, NMNZ.
A. rodolphi	120	0-40	Kermadec Is.	McKnight, 1968, Pawson, 1961, Perrier, 1875, Sladen, 1889, NZOI.
A. paschae	180	0-20	Easter Is.	Clark, 1920, Devaney, 1972, Codoceo, 1974.
A. platei	320	0-160	Juan Fernandez Is./ Desventuradas Is.	Madsen, 1956, Meissner, 1896, Codoceo, 1976.
M. gelatinosus	280	0-?	Chilean coast	Fisher, 1923, Dayton *et al.*, 1977, Madsen, 1956.

AM = Australian Museum Collection

NZOI = New Zealand Oceanographic Institute Collection

NMNZ = National Museum of New Zealand Collection

suggests also, that *Astrostole* spp. are intolerant of soft substrata. Therefore, seafloor migration by adults, in an east-west direction, is unlikely to have been responsible for this recent extension of the geographical range of these species to Australia. However, the introduction of *A. scabra* to Tasmania may have enabled this species to migrate northwards along the shallow shelf connecting Tasmania with mainland Australia. Surface current systems in the north Tasman Sea alter seasonally (Wyrtki, 1960), and in winter, currents move from the general direction of Norfolk and Lord Howe Islands towards the Australian mainland before joining the southward-moving East Australian Current. This latter surface current system may have carried larvae of *A. multispina* and *A. insularis* to Australian mainland coasts.

Fell's (1962a) West Wind Drift theory for the dispersal of the genus fails to account for the occurrence of three separate species in the supposed "donor region". At the opening of the Pliocene, an invasion of Indo-west-Pacific forms, down the Malay-Pacific archipelago, or its former equivalents (Fell, 1953a), probably resulted in the simultaneous colonisation of Lord Howe Island and Norfolk Island, and speciation there. Indeed, Briggs (1974) considered Lord Howe and Norfolk Islands part of the Indo-west-Pacific region. The New Zealand species, *A. scabra*, could have arisen simultaneously, or may have been derived from Lord Howe Island or Norfolk Island via the Lord Howe Rise or Norfolk Ridge, which were possibly shallower in former times (Fleming, 1957). The East Australian Current is probably not implicated as it did not arise until the late Pliocene (Fleming, 1951), and does not directly influence waters surrounding the two islands. Fleming (1961) presented evidence that an early Pleistocene invasion of New Zealand by molluscs from Norfolk Island took place.

The geographical distribution of the genus *Astrostole* presented here, suggests that the West Wind Drift is not the sole dispersal agency

involved. West Wind Drift can certainly transport materials great distances, as indicated by the occurrence of *Nothofagus* sp. logs from Tierra del Fuego on the shores of Macquarie Island and Tasmania (Barber *et al.*, 1959). The West Wind Drift operates south of the Sub-tropical Convergence (Dawson, 1965; Sverdrup *et al.*, 1942; Knox, 1975). The Sub-tropical Convergence has not lain north of East Cape/Taranaki since the late Pliocene (4m yrs. B.P.) and has been located farther south since the Miocene (11m yrs. B.P.) (Knox, 1975). Therefore, since the appearance of the genus, the Kermadec Islands have never been under the direct influence of the West Wind Drift, and cannot have been the first recipient outpost as designated in Fell's scheme. *A. rodolphi*, therefore, probably appeared at the Kermadecs at the same time as the colonisation of Norfolk and Lord Howe Islands occurred.

Briggs (1974) stated, "the West Wind Drift effect is most pronounced in the Sub-Antarctic region...", and Knox and Lowry (1974) considered, "the West Wind Drift to have been an important agent in the distribution of littoral faunas in the Sub-Antarctic". Although Dawson (1965) conceded that seaweed-dwelling echinoderm genera such as *Trachythyone*, *Stereoderma* and *Ocnus* may have been distributed in the West Wind Drift, he favoured seafloor migration along submarine ridges to explain present echinoderm distributions in the New Zealand Sub-Antarctic. The recent echinoderm fauna of this region is indeed drawn from the New Zealand mainland (Fell, 1953a). While the West Wind Drift may be a potent dispersal mechanism in the Sub-Antarctic zone, the faunas of Lord Howe and Norfolk Islands are primarily tropical, and the Kermadec and Juan Fernandez Islands represent "distinct provinces" (Briggs, 1974). Further, three of the four Easter Island stelleroids are wide-ranging Indo-west-Pacific species (J.F. Clark, unpublished manuscript), and therefore, although the location of the Sub-tropical Convergence (and consequently the West Wind Drift), in the

eastern Pacific, has not been established (Neumann and Pierson, 1966), it is apparent that these island outposts are too far north to have been influenced directly by the West Wind Drift.

In contrast, the southernmost parts of New Zealand are directly influenced by the West Wind Drift (Brodie, 1960) and *A. scabra*, which occurs in the area, may be the source of the easterly "cold water" Chilean representative, *M. gelatinosus*.

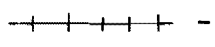
A west to east current operates north of the Sub-tropical Convergence (Sverdrup *et al.*, 1942; Dawson, 1965) and *A. rodolphi* on the Kermadec Islands may have acted as the source of the "warm water" easterly derivative, *A. platei* of the Juan Fernandez Islands, via this current.

The Peru Coastal Current developed in the early Pliocene (Fleming, 1970) and the existence of this current has precluded interchange of material between the Chilean coast and the Juan Fernandez Islands. Briggs (1974) maintained that these islands are influenced by the western edge of the current but Hay (1977) considered the islands "far beyond the influence of the narrow, cold, Peru Coastal Current". The latter view is supported by the fact that the alga *Durvillaea antarctica* is widely distributed along the Chilean coast but is absent from the Juan Fernandez Islands (Hay, 1977). The close, but discontinuous distributions of *A. platei* and *M. gelatinosus*, are also supportive of this view. *A. platei* was first recorded from the Desventuradas Islands in 1960 (Codoceo, 1976), but the history of the species at these islands is unknown. The Desventuradas Islands and Easter Island were probably colonised from the Juan Fernandez Islands by means of a surface gyre which exists in the area (Sverdrup *et al.*, 1942). This eastern Pacific surface gyre also influences the waters surrounding Pitcairn Island and Sala y Gomez, and it is possible that these islands support an as yet unknown species of *Astrostole*.

Figure 1.3 illustrates the current systems, and dispersal pathways envisaged.

Vast distances separate the western species of *Astrostole* from their eastern congeners. The only investigation of larval stages showed that the larvae of *A. scabra* could be maintained for a maximum of 63 days in optimum conditions (Maxwell, 1957). If this larval life span is typical of the genus as a whole, it seems hardly feasible that the transport of larvae could account for their observed distribution. Mortensen (1925) observed adult *Calvasterias* floating on drift algae, and this mechanism seems most likely to have accounted for the observed distribution of *Astrostole*.

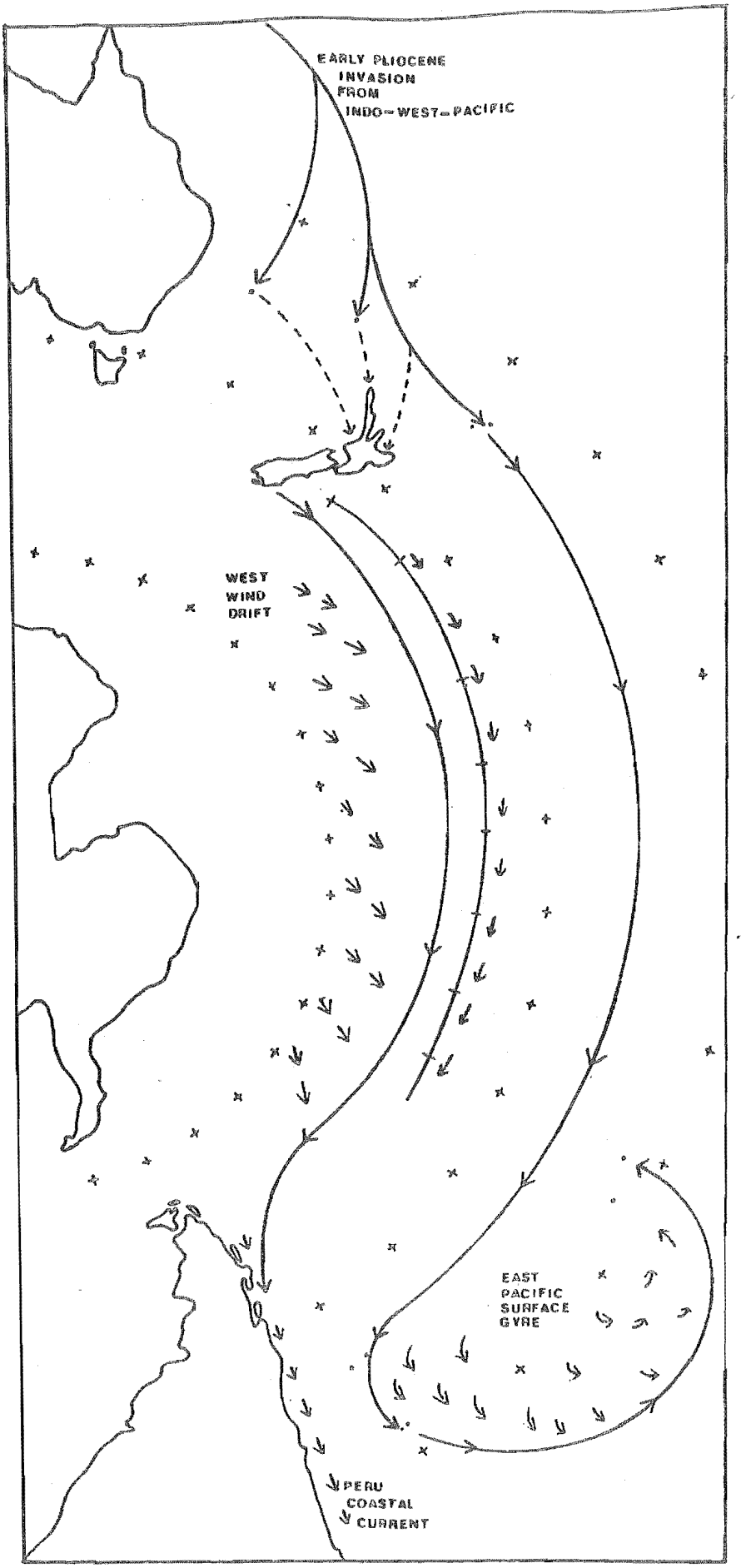
FIGURE 1.3: Suggested routes and major current systems involved in the dispersal of *Astrostole* and *Meyenaster*.


- approx. position of the Sub-tropical Convergence

- alternative migration routes to New Zealand

- migration pathways

- current systems


EARLY PLIOCENE
INVASION
FROM
INDO-WEST-PACIFIC
WEST
WIND
DRIFT
EAST
PACIFIC
SURFACE
GYRE
PERU
COASTAL
CURRENT

SECTION 2

CHAPTER 2. SOME ASPECTS OF THE POPULATION DYNAMICS OF *ASTROSTOLE SCABRA*

INTRODUCTION

A comprehensive description of the population dynamics of a species requires measurement of its growth, recruitment, mortality and migration rates. The determination of these parameters allows the erection of an age structure for the population. Growth, recruitment and mortality rates in asteroids are notoriously difficult to measure. Asteroid skeletal components do not exhibit growth lines (Smith, 1940; Feder, 1956; Hatanaka and Kosaka, 1959; Crump, 1971) and, in the absence of food, asteroids can survive for long periods with loss of body weight (Feder and Christensen, 1966; Crump, 1969; Feder, 1970). Growth in asteroids is related directly to the amount of available food (Chapter 8) and therefore, it is not possible to age or determine the growth rate of a seastar from its size (Vevers, 1949; Hancock, 1958). The use of size-frequency distributions in the estimation of asteroid age groups (Greig, 1919; Smith, 1940; B. Rasmussen, 1965) is questionable (Crump and Emson, 1978).

Recruitment rates, determined by counting newly-settled (immature) seastars, have been measured by Menge (1975) in *Pisaster ochraceous* and by Crump and Emson (1978) in *Asterina gibbosa*.

The use of vital stains (Loosanoff, 1937; Vernon, 1937; Hancock, 1958; Feder, 1970) and plastic anchor tags (Birkeland, 1974; Dayton *et al.*, 1974) has permitted the tracking of seastars and measurement of the extent to which they move. *Acanthaster planci* can move at a rate of 20m per hour, and may migrate for distances of up to 3km per month

(Endean, 1973). However, asteroids typically undertake more restricted movement of no more than about 20m per day (Galtsoff and Loosanoff, 1939; Needler, 1941; Spärck, 1952; Dayton *et al.*, 1974).

Astropecten species have characteristic daily activity patterns (Mori and Matutani, 1952; Christensen, 1970; Massé, 1966, 1975; Ferlin-Lubini and Ribi, 1978), and Ferlin (1973) discovered that *A. aranciacus* moved faster, and for longer periods on fine rather than coarse sands. Burla *et al.* (1972) noted that *A. aranciacus* returned repeatedly to their starting points, although larger individuals moved over greater distances and were less faithful to their starting points. Wilson and Marsh (1974) suspected the existence of a "home base" for *Acanthaster planci* in western Australian waters. Some remarkable observations of passive movement by asteroids appear in the literature. Loosanoff (1958) reported that *Asterias forbesi* could be carried for several feet by spurts of current, and in currents of about two knots seastars "were observed floating parallel to the bottom ..... some individuals were seen tumbling end-over-end". In very strong currents he saw seastars with the ray tips curled, forming an open ball, and they were rolled along readily by the current. Korringa (1951) noted that Dutch fishermen claimed to have seen *Asterias rubens* floating at the sea surface; a phenomenon apparently facilitated by gas production by the starfish.

Paine (1976) found little intermixing of sub-populations of *Pisaster ochraceous*, and noted that individuals would remain within an area bounded by only poorly defined barriers. As this species can adjust its body size to suit local conditions, the existence of adequate food supplies in a physiologically acceptable habitat obviates the stimulus to move away. These findings complemented those of Landenberger (1966) who reported that *P. giganteus* stayed within an area likely to yield food, learned the limits of that area and confined itself within those limits. Discontinuous spatial distributions of

adult and juvenile seastars have been demonstrated by Burla *et al.* (1972) in *Astropecten aranciacus*, Doi (1976) in *A. scopiarus*, *A. latespinosus* and *A. polyacanthus*, and A. Birtles (pers. comm.) in *A. vappa*. The factors causing this type of separation remain unclear.

The aims of this study were to determine, by tagging of individual seastars, the emigration and immigration rates, and residence periods of *A. scabra* in selected intertidal pools. The radius and eviscerated wet weight of both intertidal and subtidal seastars were measured to reveal if any differences existed in their size and morphology, and to provide data for the indirect estimation of recruitment and growth rates, longevity and age at first spawning.

MATERIALS AND METHODS

Preliminary laboratory trials undertaken to assess the suitability of plastic anchor tags for marking seastars showed these devices to be entirely unsuitable. Seastars were unavoidably wounded by the insertion of such tags, and within 48h punctured rays were autotomised, or the skeleton surrounding disc wounds decayed, allowing the tag to fall out. Kvalvagnaes (1972) encountered identical problems when he attempted to tag *Asterias rubens*. Laboratory trials with vital stains proved successful and this marking method was adopted.

Between May 1977 and February 1978, individual *A. scabra* were stained in the field with a 1g per litre solution of Nile Blue sulphate which was taken up by the tube feet and adambulacral spines. The stain was retained for up to six months, but was reinforced whenever seastars were recaptured. Individual rays were stained selectively and many combinations could be obtained by using the madreporite as a reference point. Thus, individual starfish were recognisable.

Two pools at First Bay, on the eastern face of Kaikoura Peninsula, were selected for recapture experiments because they contained seastars

throughout the year, had restricted access to the open sea, were subjected to minimal public disturbance, and rocks under which seastars occurred were large, individually identifiable, and immobile. Site 1A, a long, shallow gully at the southern end of First Bay, was 45m in length, 0.1 - 2.0m wide, and no more than 1m deep during low tide (Fig. 2.1). Site 1B, a roughly rectangular pool at the northern end of First Bay, measured 12.9m x 10.2m, and was also no more than 1m deep during low tide (Fig. 2.2).

Each pool was visited at least once per month and the number of stained and unstained animals beneath rocks noted. Immigrants were stained. Immigration and emigration rates and the number of seastars resident between inspection periods were then determined. The movement of resident starfish at each site was measured by reference to a permanent bedrock feature with a 30m fibreglass tapemeasure.

As the volume of coelomic fluid in intact individual starfish may vary (Feder, 1970), eviscerated wet weight is a more reliable measure of size in seastars (Crump and Emson, 1978), and was the method adopted here. The determination of seastar dry weight was unnecessary as it became clear early in the study that eviscerated wet weight and starfish radius were closely correlated. Intertidal seastars used to obtain radius and eviscerated wet weight data were collected from the sites described in detail in Chapter 4 between July 1975 and October 1977. Subtidal specimens were collected during the same period from baited rock-lobster traps set overnight at depths of 20-146m within 2km of the southern, eastern and northern shores of Kaikoura Peninsula. The radius (R) of seastars was measured with vernier calipers from the proximal edge of the madreporite to the tip of the opposite ray.

The size-frequency distribution of *A. scabra* was analysed by a modified probability paper method (Cassie, 1954). The normal curves obtained from this analysis were superimposed on the size-frequency

FIGURE 2.1: Site 1A, a long shallow gully at the southern end of First Bay.

FIGURE 2.2: Site 1B, a rectangular pool at the northern end of First Bay.

distribution and verified by the Kolmogorov-Smirnov Dmax test (Siegel, 1956).

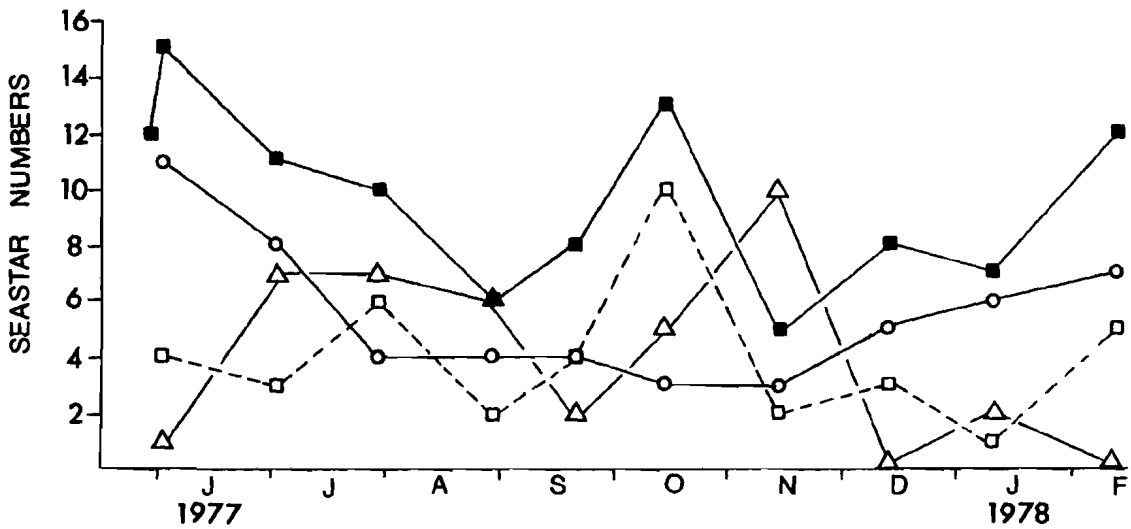
RESULTS

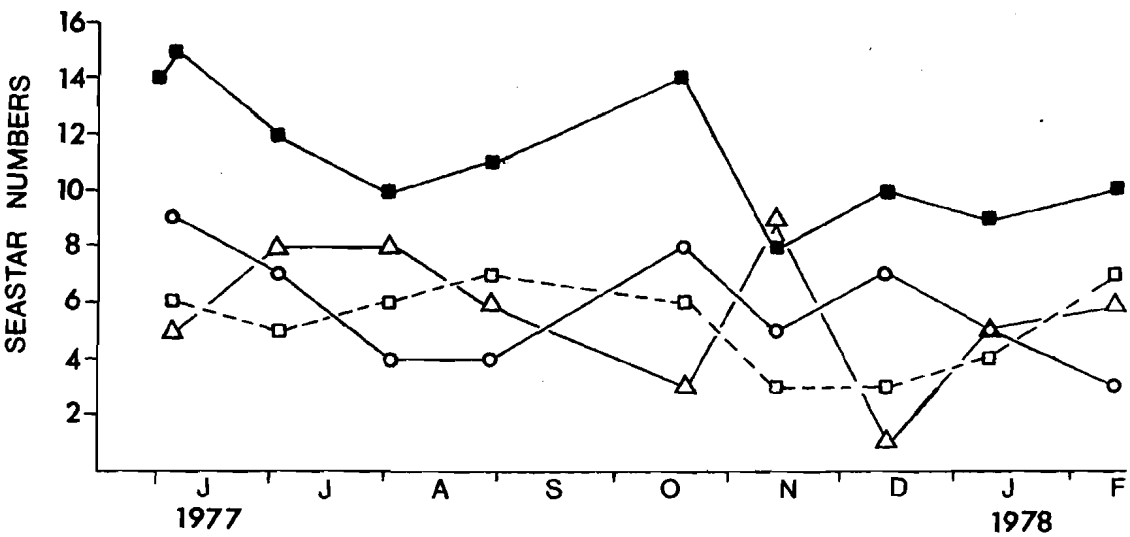
Movement

The number of seastars resident at any time was similar at sites 1A and 1B with maxima of 15 (both sites) and minima of 5 and 8 respectively (Fig. 2.3). At site 1A, emigration exceeded immigration from mid-June until late August so that total numbers fell. An identical situation was found at site 1B until early August. Total numbers rose at both sites until mid-October, fell until mid-November, and rose again at both sites until the end of sampling in February 1978. Emigration was highest from mid-October to mid-November at both sites when 10 and 9 seastars respectively departed. Immigration was low during this period (2 and 3 seastars respectively) when most seastars were residents.

Emigration, immigration and residency bore similar relationships to each other at both sites in all but five sampling periods (early July, late August, mid-October, mid-January and mid-February), so although total numbers at both sites reached high levels in mid-October, at site 1A this was due to immigration whereas at site 1B residents formed the majority of total numbers. At both sites, total numbers were related inversely to emigration. At site 1A, total numbers were related directly to immigration, but this relationship was less pronounced at site 1B. The opposite was true of the relationship between resident and total numbers which were correlated directly at site 1B but which had less mutual influence at site 1A. There was no evidence of seasonal inshore or offshore migration. The general pattern at both sites was of moderate fluctuations in emigrant, immigrant and

FIGURE 2.3: Stained (O), immigrant (□), emigrant (△), and total (■) numbers of *A. scabra* at sites 1A (upper) and 1B (lower) between June 1977 and February 1978.


SEASTAR NUMBERS
16
14
12
10
8
6
4
2
J
J
A
S
O
N
D
J
F
1977
1978


SEASTAR NUMBERS
16
14
12
10
8
6
4
2
J
J
A
S
O
N
D
J
F
1977
1978

resident numbers.

Most seastars remained resident in the two intertidal pools for less than 30 days and the majority of tagged specimens had left before the next site inspection (Figs 2.4, 2.5). In some cases they reappeared in subsequent searches. At site 1A, seastars were never recovered more than 107 days after tagging, and only four specimens were recaptured more than four times. At site 1B, three seastars were recovered 192 days after tagging but only four specimens were recaptured three or more times. The maximum number of recoveries of a single seastar in consecutive inspections was six at site 1A and three at site 1B. At neither location were any animals tagged in June 1977 still present in February 1978. There was no intermixing of individuals between the two sites.

The patterns of locomotion in seastars recaptured three or more times (Figs 2.6, 2.7) record only the net change in location of resident individuals between sampling periods and are likely to underestimate the extent of movement. These data reveal that resident specimens undertook extensive movement about the pools but did not appear with any pronounced regularity beneath the same rocks. Seastars 3 and 20 were recorded from beneath the same rock on two or more occasions, but it cannot be demonstrated that they did not move at all, or that they displayed a "homing" instinct for these locations. Recoveries made between non-consecutive searches support the contention that these specimens emigrated from the pool only to return later. The largest net change in location recorded for a resident seastar in consecutive searches was 13.5m (seastar 25 between 2 July and 8 August 1977) (Fig. 2.7). Five types of movement could be recognised with respect to a pool; immigration, permanent emigration, temporary emigration, net movement within the pool and no movement. Most specimens emigrated permanently. Except in early July, resident seastars at site 1B consistently moved

FIGURE 2.4: Numbers of *A. scabra* tagged and remaining from previous taggings on dates shown at site 1A.

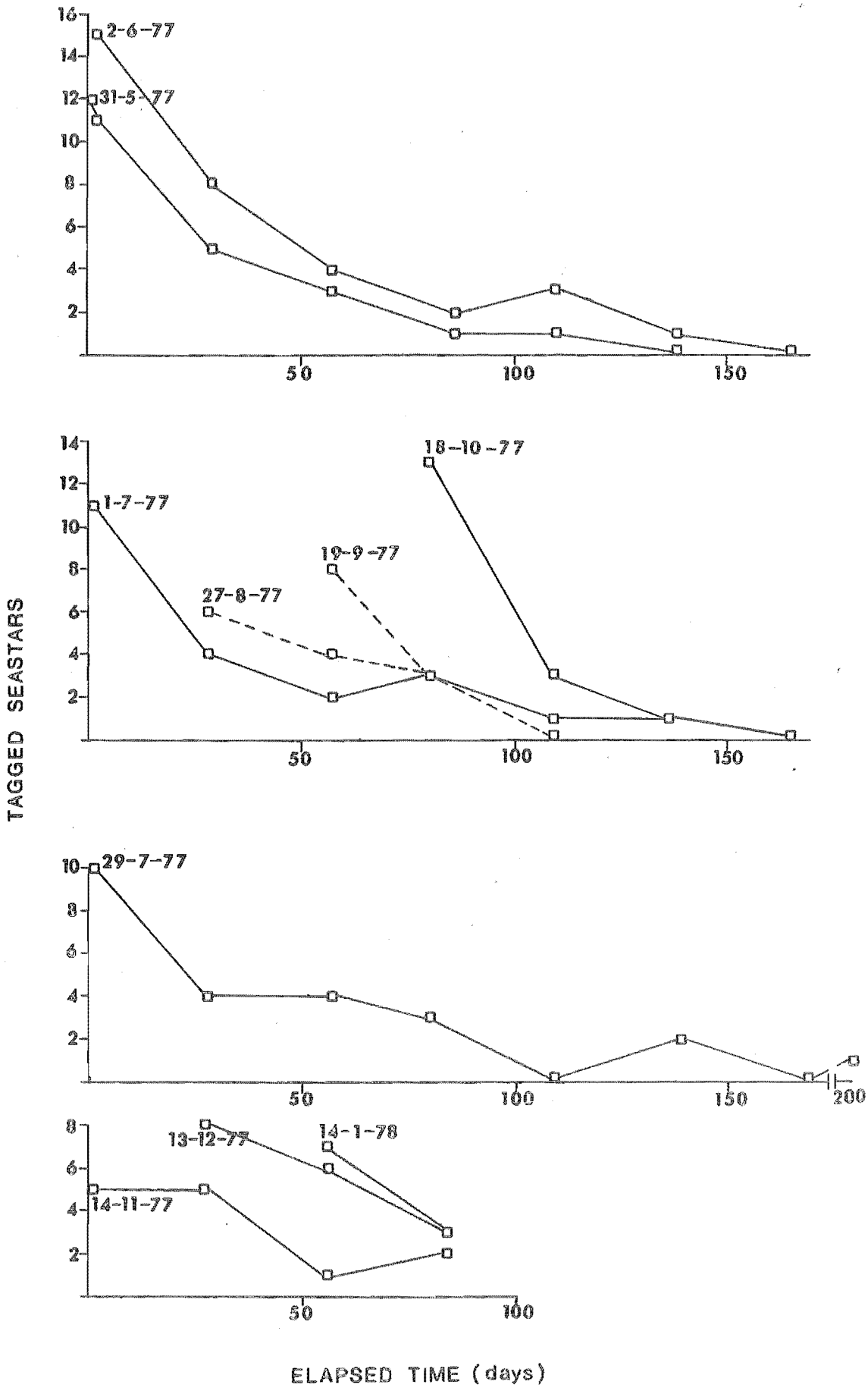

2-6-77
31-5-77
1-7-77
18-10-77
19-9-77
27-8-77
29-7-77
13-12-75
14-1-78
14-11-77
TAGGED SEASTARS
ELAPSED TIME (days)

FIGURE 2.5: Number of *A. scabra* tagged and remaining from previous taggings on dates shown, at site 1B.

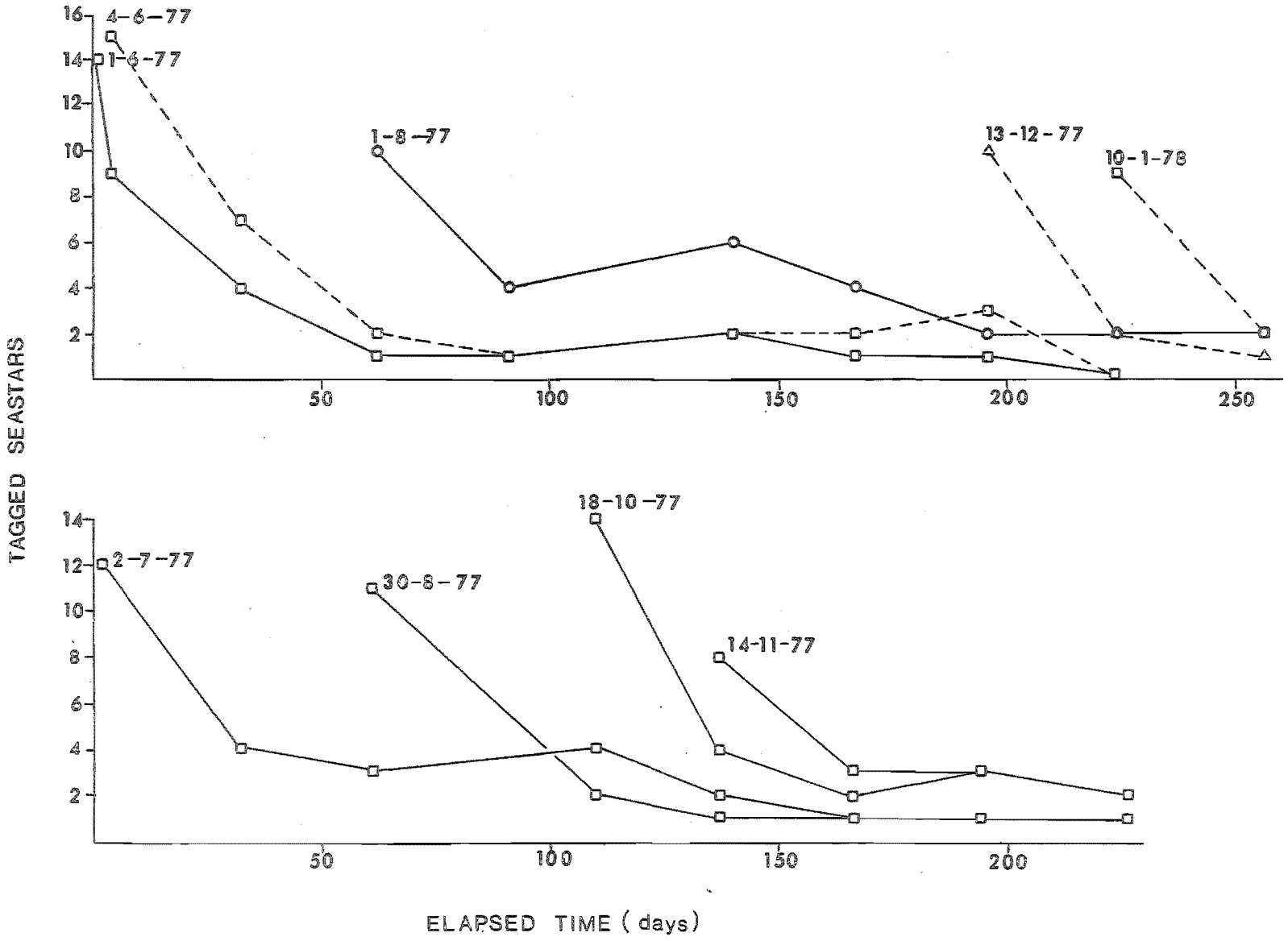

TAGGED SEASTARS
4-6-77
1-6-77
1-8-77
13-12-77
10-1-78
2-7-77
30-8-77
18-10-77
14-11-77
ELAPSED TIME (days)

FIGURE 2.6: Diagrammatic representations of the patterns of locomotion of four *A. scabra* recaptured four or more times between consecutive (solid line) and non-consecutive (hatched line) searches at site 1A.

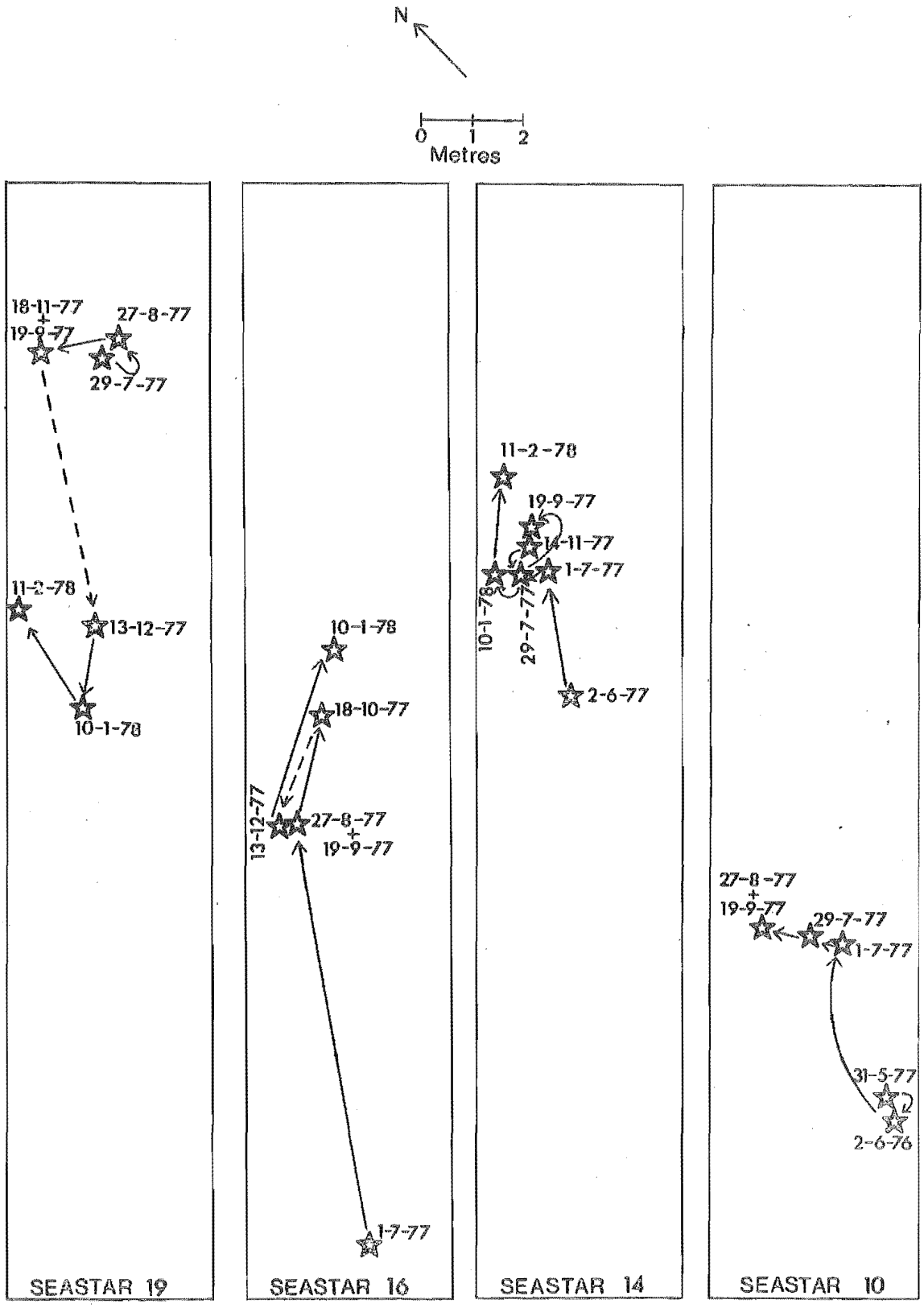

N
0 1 2
Metres
18-11-77
+
19-9-77
27-8-77
29-7-77
11-2-78
13-12-77
10-1-78
SEASTAR 19
10-1-78
18-10-77
13-12-77
27-8-77
+
19-9-77
1-7-77
SEASTAR 16
11-2-78
19-9-77
14-11-77
1-7-77
10-1-78
29-7-77
2-6-77
SEASTAR 14
27-8-77
+
19-9-77
29-7-77
1-7-77
31-5-77
2-6-76
SEASTAR 10

FIGURE 2.7: Diagrammatic representation of the patterns of locomotion of four *A. scabra* recaptured three or more times between consecutive (solid line) and non-consecutive (hatched line) searches at site 1B.

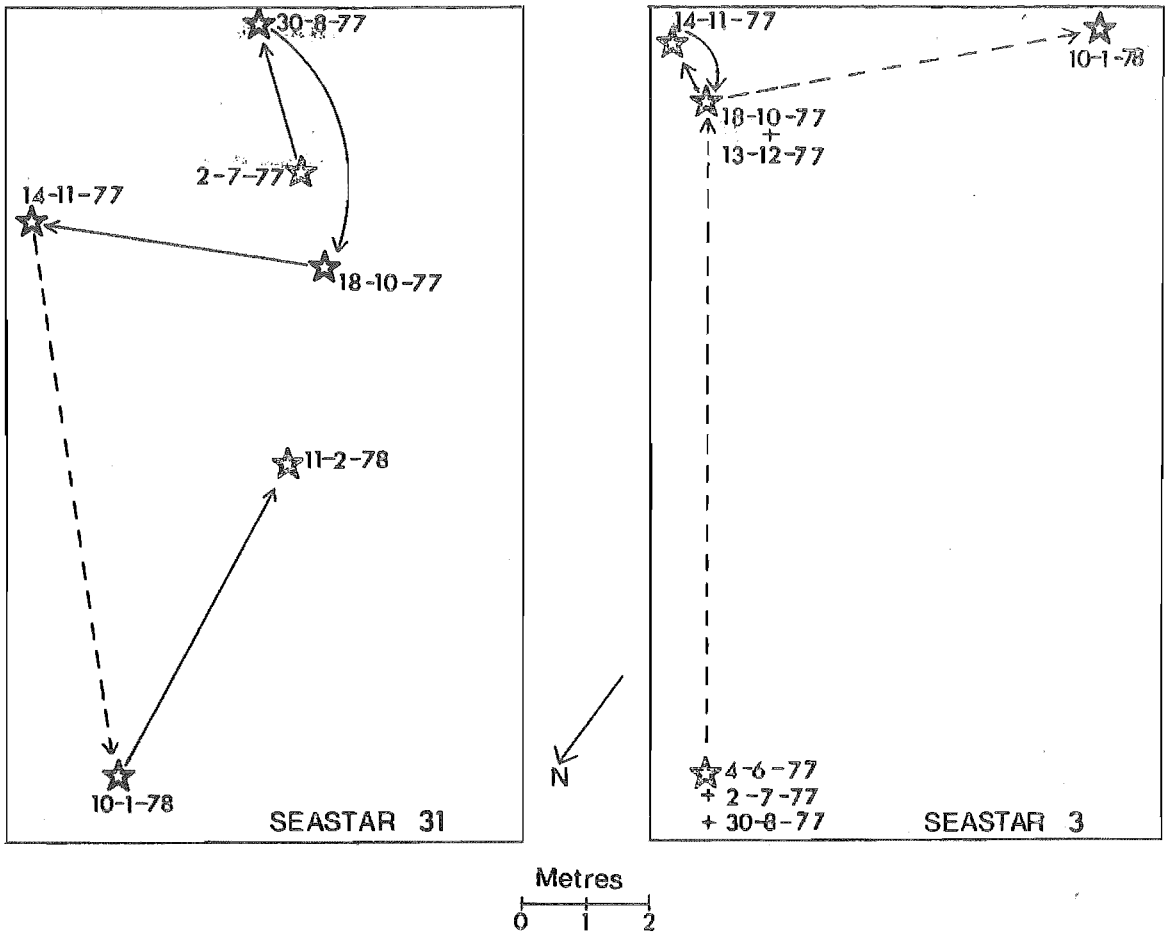

30-8-77
2-7-77
14-11-77
18-10-77
11-2-78
10-1-78
SEASTAR 31
N
14-11-77
10-1-78
18-10-77
+
13-12-77
4-6-77
+ 2-7-77
+ 30-8-77
SEASTAR 3
Metres
0 1 2
14-11-77
2-7-77
+
1-8-77
4-6-77
SEASTAR 20
14-11-77
1-8-77
13-12-77
18-10-77
2-7-77
SEASTAR 25

TABLE 2.1. Net distances moved (m) by resident *A. scabra* between site inspections.

Date	TIME BETWEEN SITE INSPECTIONS (DAYS)	MEAN NET DISTANCE MOVED SITE 1A	SITE 1B
1-7-77	2	5.86	1.77
29-7-77	28	0.81	6.12
27-8-77	28	0.21	4.42
19-9-77	22	0.3	-
18-10-77	28	0.8	4.34
14-11-77	26	4.3	5.8
13-12-77	28	4.2	4.6
10-1-78	27	3.9	5.5
11-2-78	31	3.4	3.8

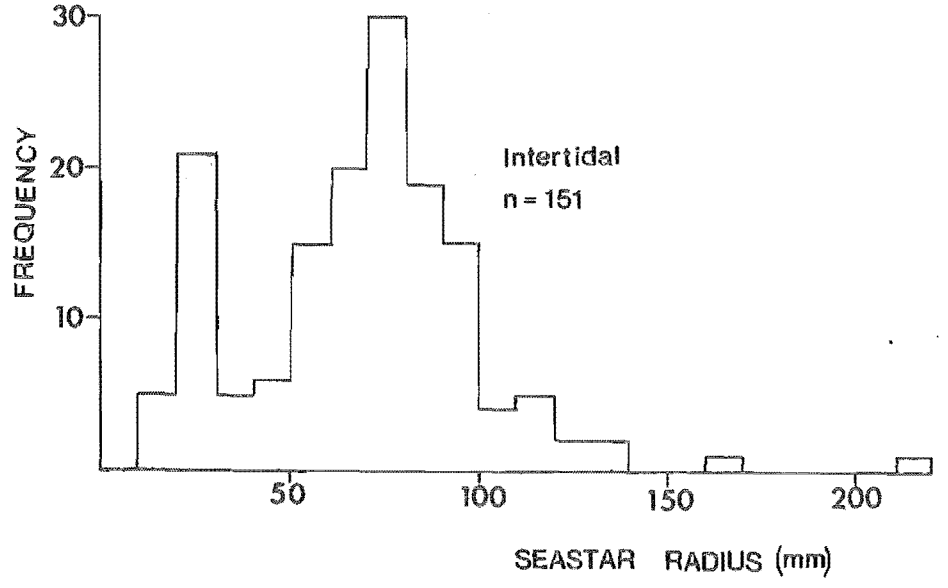
greater net distances than those at site 1A (Table 2.1). The long, narrow structure of the site 1A pool meant that potential movements of seastars were more restricted than they were at site 1B. These results demonstrate that *A. scabra* is a moderately mobile species and, although individuals sometimes remained resident within a specific area, they showed little site-specificity.

Size and morphology

Size-frequency distributions of intertidal and subtidal *A. scabra* at Kaikoura differed markedly (Fig. 2.8). Few specimens of R >140mm appeared in intertidal collections (Fig. 2.9), whereas all animals collected from depths of 20-146m exceeded R = 110mm. Thus there was a distinctly discontinuous distribution of large and small specimens of *A. scabra* in terms of both space and depth. This separation was based not only on size, but also on sexual maturity. The smallest mature seastar encountered in this study had R = 110mm (Chapter 3). Subtidal seastars also had fewer regenerating rays than intertidal specimens (Table 2.2).

Eviscerated wet weight and seastar radius were correlated significantly in intertidal specimens (Fig. 2.10). However, once seastars had reached R = 110mm the eviscerated wet weight - radius characteristics of intertidal and offshore specimens diverged (Fig. 2.11). For a given radius, seastars taken from depths of 20-146m were lighter than intertidal individuals (ANCOVA on slope of regression lines in Fig. 2.11, $F = 7.70$, $p < 0.01$). *A. scabra* from offshore locations were more liberally supplied with pedicellariae, had lighter pigmentation, but most importantly had thinner skeletons than their intertidal counterparts. The latter was the prime cause of the observed differences in size-weight characteristics.

FIGURE 2.8: Size frequencies of intertidal and subtidal (20-146m depth) *A. scabra* measured in October 1976 (n = sample size).


30
20
10
FREQUENCY
Intertidal
n = 151
50
100
150
200
SEASTAR RADIUS (mm)

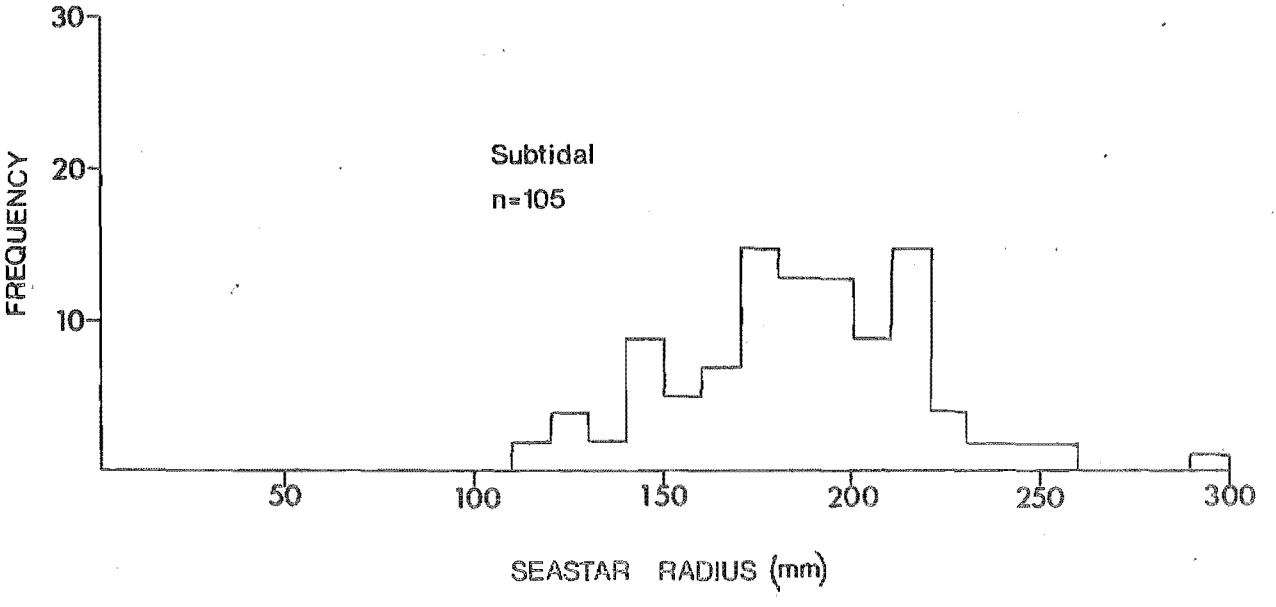

30
20
10
FREQUENCY
Subtidal
n=105
50
100
150
200
250
300
SEASTAR RADIUS (mm)

FIGURE 2.9: Size frequencies (%) of intertidal *A. scabra* measured at monthly intervals (n = sample size).

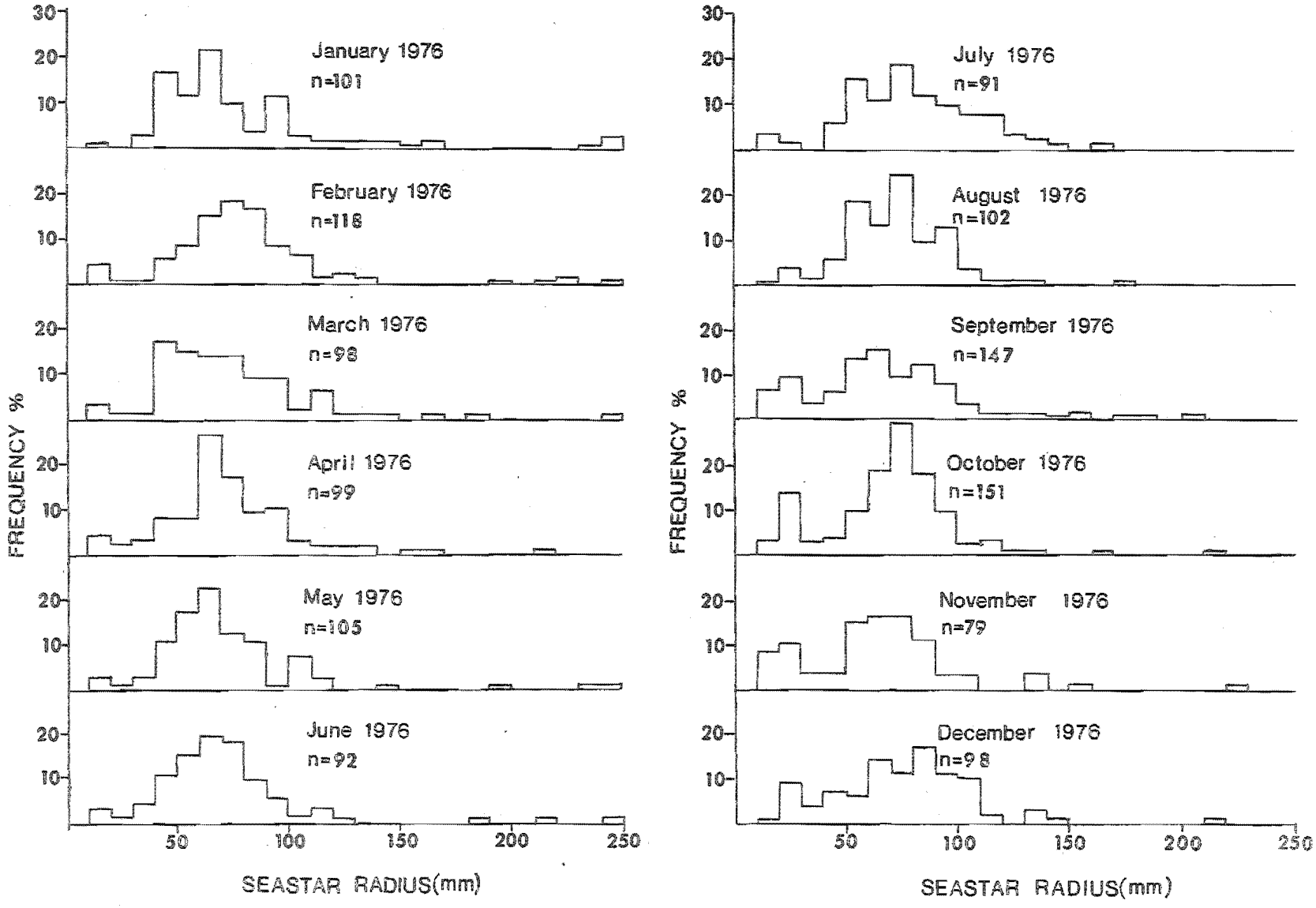

January 1976
n=101
February 1976
n=118
March 1976
n=98
April 1976
n=99
May 1976
n=105
June 1976
n=92
July 1976
n=91
August 1976
n=102
September 1976
n=147
October 1976
n=151
November 1976
n=79
December 1976
n=98
FREQUENCY %
SEASTAR RADIUS(mm)
SEASTAR RADIUS(mm)

TABLE 2.2. Numbers of intertidal and subtidal *A. scabra* regenerating lost rays in October 1976 (n = sample size).

NO. OF RAYS REGENERATING	SEASTAR NUMBERS	
	INTERTIDAL (n = 151)	20-146m (n = 105)
1	12	5
2	6	2
3	2	1
4	4	1
5	2	-
6	3	-
TOTAL	29	9
% OF SAMPLE	19.2	8.5
% REGENERATING 1 RAY	41.3	55.5

TABLE 2.3. Year classes derived from analysis of size-frequency data for intertidal and offshore *A. scabra* collected in October 1976.

YEAR CLASS	SIZE RANGE (R, mm)	MEAN SIZE (± S.D.)
1+	10-40	24.1 (± 4.66)
2+	30-110	72.1 (± 16.8)
3+	100-160	129.2 (± 18.1)
4+	150-210	181.7 (± 14.9)
5+	200-260	218.3 (± 14.1)
6+	250+	-

FIGURE 2.10: Relationship between eviscerated wet weight and radius in intertidal *A. scabra*. Regenerating seastars omitted.

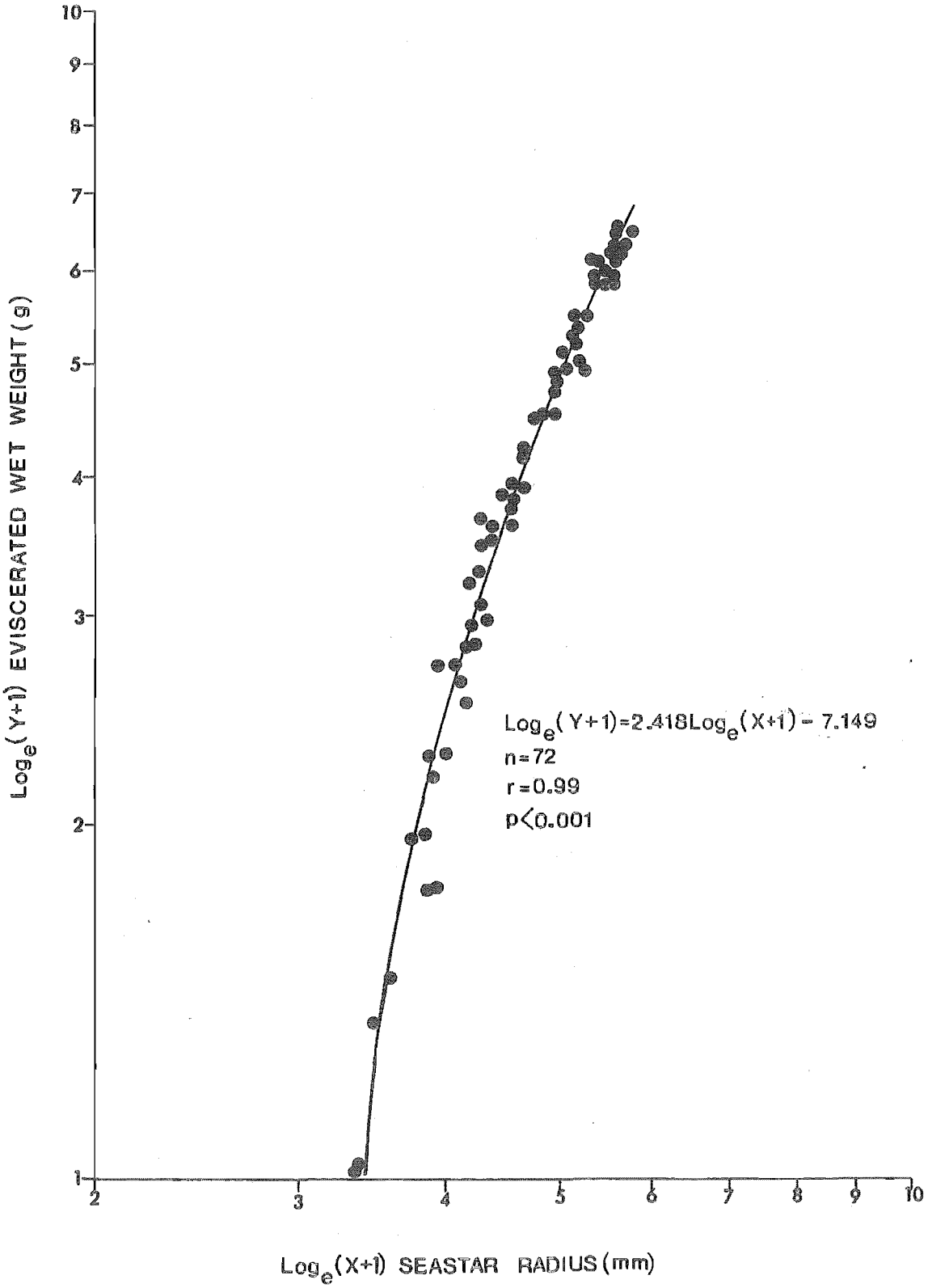
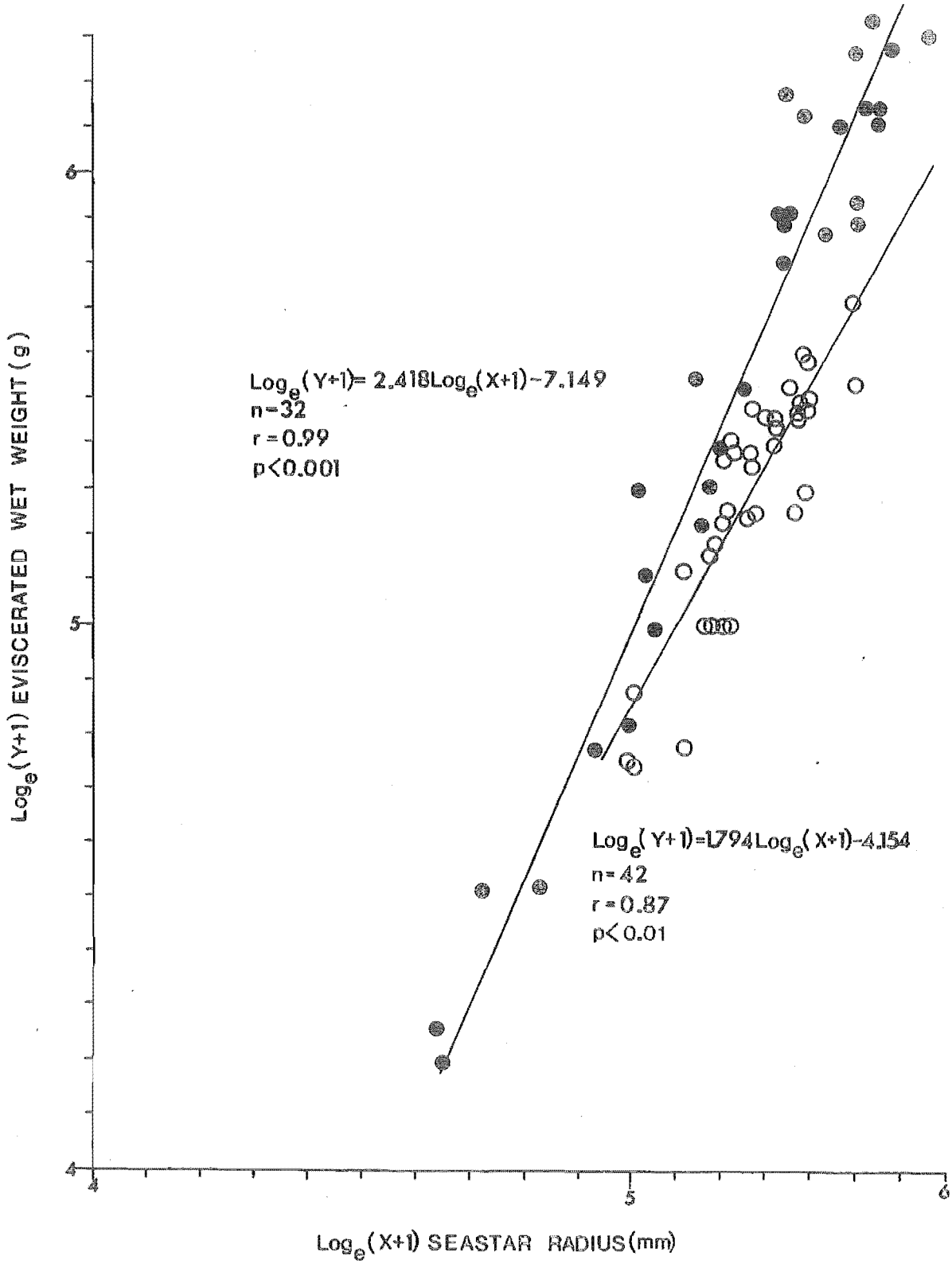

Log$_e$(Y+1) EVISCERATED WET WEIGHT (g)
Log$_e$(X+1) SEASTAR RADIUS (mm)
Log$_e$(Y+1)=2.418Log$_e$(X+1) - 7.149
n=72
r=0.99
p<0.001

FIGURE 2.11: Relationship between eviscerated wet weight and radius in intertidal (●) and subtidal (o) *A. scabra* exceeding R = 110mm collected in October 1976. Regenerating seastars omitted.


Log$_e$(Y+1) EVISCERATED WET WEIGHT (g)
Log$_e$(X+1) SEASTAR RADIUS (mm)
Log$_e$(Y+1)= 2.418Log$_e$(X+1)-7.149
n=32
r=0.99
p<0.001
Log$_e$(Y+1)=1.794Log$_e$(X+1)-4.154
n=42
r=0.87
p<0.01
4
5
6
4
5
6

Growth, recruitment, mortality and longevity

Probability paper analysis of the combined size-frequency distribution of 256 intertidal and offshore *A. scabra* collected in October 1976, when the smallest specimens (R = 10-40mm) were most numerous (Fig. 2.9), and must have been at least one year old (Chapter 3), formed four distinct points of inflexion (Fig. 2.12) and suggested the presence of at least five size (age) classes (Fig. 2.13). The largest seastars (R > 360mm) were exclusively intertidal and could not be aged. The smallest, sexually mature, offshore specimens belonged to the 3+ year group. This agrees well with the estimate derived from Menge's (1975) method (using data from site 1, Chapter 4, collected in October 1976):

$$\text{Longevity} = \frac{\text{Overall population density } (m^{-2})}{\text{Density of recruits } (m^{-2})} = \frac{0.08507}{0.0274} = 3.1 \text{ yrs,}$$

except that in this case, the result is the mean length of the intertidal phase of life and not mean longevity. Recruitment, as measured by the density of 1+ year class (R = 10.40mm) animals, occurred at a rate of 2.74 seastars per $100m^2$ of shore per year. This may be an underestimate, as animals of this size were extremely difficult to find. It can be concluded that *A. scabra* lives for about three years in the intertidal zone where it grows up to R = 110mm (Table 2.3) before migrating to deeper waters and attaining sexual maturity. These estimates of age must be viewed as conservative because the smallest seastars may in fact be two years old, and the large R = 30-110mm size class may be composed of individuals from a number of year classes with normally distributed size-frequency characteristics.

Mortality is the most difficult parameter to measure. Over 19% of intertidal seastars collected in October 1976 were in the process of regenerating lost rays, and after severe storms it was not unusual to find parts of the intertidal zone littered with autotomised rays. However, only once, in February 1976, was a seastar found crushed

FIGURE 2.12: October 1976 size frequency data for *A. scabra* subjected to Cassie's (1954) modification of probability paper analysis.

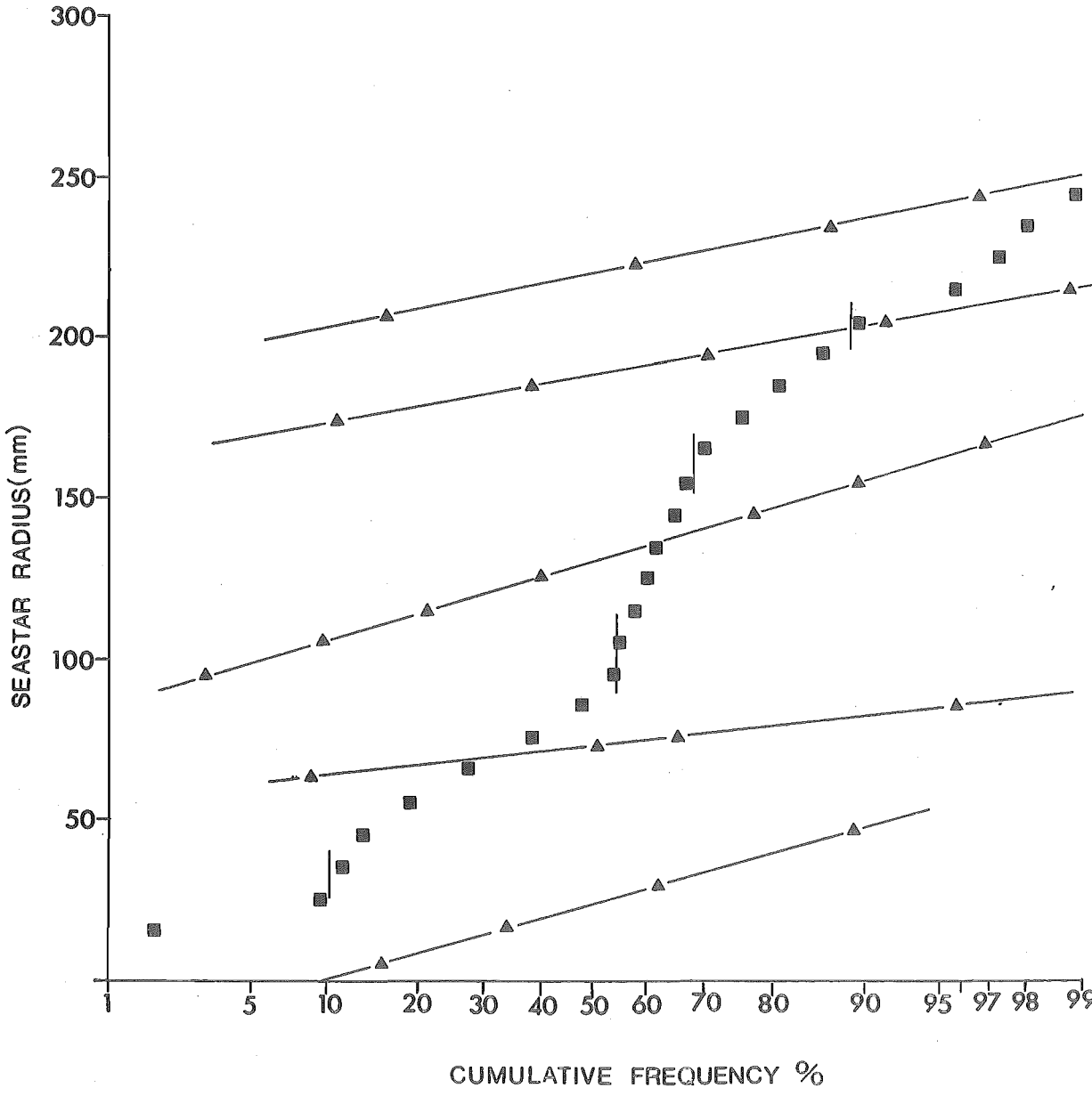
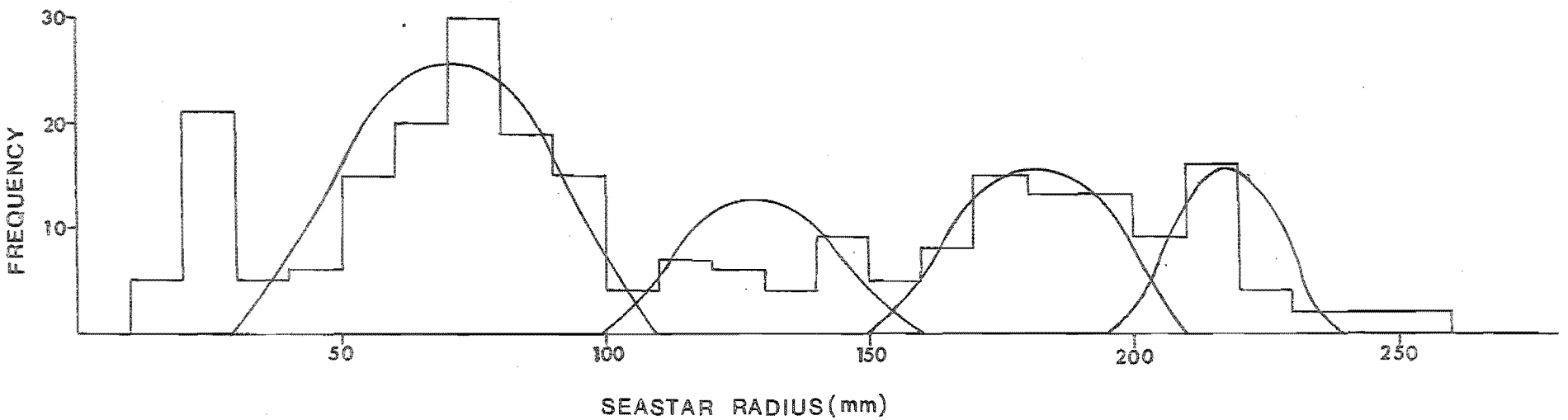

300
250
200
150
100
50
SEASTAR RADIUS(mm)
1
5
10
20
30
40
50
60
70
80
90
95
97
98
99
CUMULATIVE FREQUENCY %

FIGURE 2.13: Size-frequency data for offshore and intertidal *A. scabra* collected in October 1976. Superimposed are normal curves derived from Cassie analysis.



K-S Dmax	K-S Dmax	K-S Dmax	K-S Dmax	K-S Dmax
= 0.217	= 0.04	= 0.26	= 0.1	= 0.36
n = 28	n = 111	n = 30	n = 56	n = 25
$p < 0.01$	$p < 0.01$	$p < 0.01$	$p < 0.01$	$p > 0.05$

beyond all possibility of regeneration.

DISCUSSION

Net movement of seastars recorded between consecutive searches is additional to a tidal pattern of foraging activity (Chapter 4). There was no evidence to suggest that seastars return to a "home base" between foraging periods, or that they learn the limits of a particular location and confine themselves within those limits. Emigrant, immigrant and resident numbers probably reflect random movements, as seastars displayed little faithfulness to single resting spots, and most individuals remained within a single pool for less than 30 days (Figs 2.4, 2.5). The handling and dyeing of seastars may have induced exaggerated movement and caused increased emigration. At neither study site did seastar numbers exceed 15 during this study, a maximum which may have been imposed by the limited number of acceptable under-boulder refuges which, however, were never fully occupied. Alternatively, this might reflect the maximum number of seastars each site can support before overcrowding and competition for food become limiting. Food abundance is unlikely to limit seastar numbers (Chapter 8) and it is unclear why individuals should not remain in locations such as these which contain an acceptable amount of food and low-tide resting points. No seasonal vertical migration, as noted in other seastars (O'Donoghue, 1924; Lewis, 1964; Mauzey, 1966; Menge and Menge, 1974), was detected, but *A. scabra* may exhibit such behaviour in other parts of its geographical range, as movement of this sort varies with latitude (Feder, 1970).

Menge (1975) considered that two areas in which 68% and 59% respectively of *P. ochraceous* were immature were "nursery areas" or sites of dense larval settlement. On this basis, the whole of the intertidal zone at Kaikoura could be considered a nursery area as

A. scabra does not become sexually mature until R $\geq$110mm (Chapter 3), and only 11.4% of intertidal specimens exceeded R = 110mm (Fig. 2.9). It can be argued that rock-lobster traps, because of their large mesh, did not catch small seastars. However, *A. scabra* caught in this way clung tenaciously to the bait, and could be removed only with great force i.e. they did not "drop off" when the trap was raised. Moreover, large seastars of R = 70-100mm, which would have been retained by the mesh, were never caught at depths of 20-146m. It is clear, that intertidal (immature) *A. scabra* undertake extensive movement within intertidal and shallow sublittoral zones, but do not venture beyond depths of 20m.

Bathymetric separation of mature and immature *A. scabra* could be caused by several factors. *A. scabra* may settle only in the intertidal zone and at depths up to 20m, or seastars which metamorphose in waters deeper than 20m might be eliminated by predation. The quantity or quality of food in the intertidal zone may be incapable of supporting large, reproductive animals, and it is noteworthy that large intertidal specimens had lower gonad indices than subtidal seastars (Chapter 3). These large, thick-skeletoned, intertidal individuals may never have migrated offshore, or may have returned to the intertidal zone after a reproductive phase, and become senile. Thorson (1946) found very large *Asterias rubens*, with shrunken gonads, in the Øresund and concluded that these were senile individuals. There are not enough large under-boulder refuges in the intertidal zone to harbour extensive numbers of mature animals, and the constant residence of mature *A. scabra* in subtidal waters reduces potential intraspecific competition for food and space in the intertidal zone. Offshore seastars have increased feeding (immersion) time, and reproductive potential is probably enhanced by increased food intake. Reproductive potential is reduced if regeneration is proceeding (Chapter 3) and the incidence of regeneration found in offshore animals was less than half that in intertidal

A. scabra (Table 2.2). Further, the majority of damaged offshore seastars were regenerating only one ray compared with two or more rays in damaged intertidal individuals. Offshore *A. scabra* are less liable to injury by rolling boulders than are intertidal seastars. Some rays could be damaged by rock-lobster traps falling from above, or by some form of attempted predation.

The absence of rolling boulders in deep waters not only reduces injury rates, but also allows the observed reduction in skeleton thickness in offshore seastars. This in turn permits the diversion of a larger portion of energy intake into gonad production. The accumulation of mature *A. scabra* between 20 and 146m enables spawning to proceed regardless of tidal influences, and concentrates mature individuals into a relatively narrow depth stratum, increasing the likelihood that spawned gametes will meet (Atwood, 1973; Ormond *et al.*, 1973).

Paine (1976) discovered that sub-populations of *P. ochraceous* had different mean sizes dependent on seastar density and the abundance and type of food present. He reported further than an improvement in food supply led to a rapid increase in size, and that individual seastars might migrate to areas best suiting their metabolic needs. He concluded that a seastar had two options; growth could be adjusted to suit local conditions, or the individual could migrate when its metabolic needs surpassed the ability of the local environment to support them. Paine's results demonstrated that *P. ochraceous* adjusted its body size, but *A. scabra* appears to migrate to deep waters once R = 110mm. Some adjustment in body size occurred through the reduction of skeleton thickness once individuals had migrated (Fig. 2.11), but sexual maturity in *A. scabra* must obviously depend on the abundance and quality of offshore food. Physical and biotic factors prevailing in the intertidal zone at Kaikoura apparently preclude the residence of *A. scabra*

large enough to become mature, i.e. if seastars did not migrate, the mean size of the intertidal population would stabilise around a value at which immaturity would be sustained.

The estimate of longevity in *A. scabra* obtained in this study is within the range determined for other species. These estimates range from 2 years in *Asterias rubens*, to 100+ years in *Odontaster validus* (Table 2.4). The growth rates required by this longevity estimate are not unduly rapid. One-plus year group *A. scabra* had a mean radius of 24.1mm (Table 2.3). The New Zealand forcipulate *Stichaster australis* can reach a radius of 25mm in 18 months (Dr M.F. Barker, pers. comm.). Ursin (1960) regarded *A. rubens* of R = 25-29mm as 1+ year group animals, whereas Orton and Fraser (1930) reported that this species could reach R = 50mm in one year, and R = 75mm in two years. Yamaguchi (1973) reported radii of 15-79mm in one year old *Acanthaster planci*. Two-plus year class *A. scabra* had a mean radius of 72.1mm, and a size range of R = 30-110mm (Table 2.3). In comparison, Fenchel (1965) recorded a size of up to R = 100mm in two year old *Luidia sarsi*, and Needler (1941) considered *Asterias vulgaris* of R = 31mm to be two years old.

A. scabra probably becomes sexually mature during its fourth year. This compares with estimates of between one and six years for other species (Table 2.5).

If indeed *A. scabra* of R = 10-40mm represent one settlement, then they account for about 11% of all seastars collected in October 1976. This must be an overestimate, as sampling of offshore animals with baited traps probably collects only a small portion of mature specimens. Menge (1975) calculated that annual mortality of larval *P. ochraceous* exceeded 99.999%, and Crump and Emson (1978) estimated that about 4% of *Asterina gibbosa* eggs actually became juvenile starfish. Little evidence of significant mortality in intertidal *A. scabra* was found although it is likely that some are killed by the grinding of

TABLE 2.4. Estimates of asteroid longevity.

SPECIES	LONGEVITY (YRS)	SOURCE
Astropecten irregularis	9+	Christensen (1970)
Astropecten armatus	5	MacGintie and MacGintie (1949)
Luidia ciliaris	3-4	Clark (1962)
Luidia sarsi	4-5	Fenchel (1965)
Odontaster validus	100+	Pearse (1969)
Nepanthia belcheri	4+	Kenny (1969)
Asterina gibbosa	5+	Crump and Emson (1978)
Pisaster ochraceous	20	MacGintie and MacGintie (1949)
Pisaster ochraceous	34+	Menge (1975)
Asterias amurensis	4+	Hatanaka and Kosaka (1959)
Asterias rubens	5-6+	Clark (1962), Bull (1934)
Asterias rubens	2	Ursin (1960)
Asterias rubens	2+	Orton and Fraser (1930)
Asterias forbesi	2+	Galtsoff and Loosanoff (1939)
Asterias vulgaris	2+	Needler (1941)
Acanthaster planci	8+	Endean (1973)

TABLE 2.5. Estimates of age at first maturity in various asteroids.

SPECIES	AGE (YRS.) AT FIRST MATURITY	SOURCE
Luidia sarsi	1	Fenchel (1965)
Ondontaster validus	3-6	Pearse (1969)
Asterina gibbosa	2	Crump and Emson (1978)
Asterias amurensis	1	Hatanaka and Kosaka (1959)
Asterias rubens	5-6	Bull (1934)
Asterias vulgaris	1	Needler (1941)
Asterias forbesi	1-2	Galtsoff and Loosanoff (1939)
Pisaster ochraceous	5	Menge (1975)
Acanthaster planci	3	Lucas (1974)

rocks during storms. Intertidal seastars regenerating lost rays were animals which had survived injury. It is assumed traditionally that asteroid populations are regulated by intense losses during larval phases due, at least in part, to the activities of planktonic carnivores. Although coral, decapod larvae, and barnacles are reported to eat asteroid larvae (Thorson, 1946; Yamaguchi, 1973; Mileikovsky, 1974), Yamaguchi (1975) concluded that asteroid larvae in general seemed to be free from predation in the open sea. The loss of larvae through dispersal is suggested as the prime cause of mortality. *A. scabra* is stenobathic and restricted to hard substrata (Chapter 1), and larvae transported to deep waters or soft substrata would probably perish. Partial immunity from these fates is conferred by the ability to delay metamorphosis. Although Birkeland *et al.* (1971) reported that *Mediaster aequalis* larvae could delay metamorphosis for up to 14 months in the absence of suitable substrata, the two to four weeks determined by Gemmill (1914) for *Asterias rubens* and by Barker (1977a) for *Stichaster australis* and *Coscinasterias calamaria* is probably more typical. Strict substrate requirements (Barker, 1977b), cannabalism (Galtsoff and Loosanoff, 1939), and food availability (Mead, 1900; Birkeland, 1974) can also influence survival in late larval and immediate post-metamorphic seastars. Apart from senescence, the causes of mortality in large *A. scabra* are unknown. Crabs (Bull, 1934; Aldrich, 1976), lobsters (Vasserot, 1965), shrimps (Wickler and Siebt, 1970), molluscs (Endean, 1973; Branham, 1973; Talbot and Talbot, 1971), seastars (Mauzey *et al.*, 1968), fish (Quast, 1971; Branham, 1973) and seabirds (Ebling *et al.*, 1966; Thomas and Thomas, 1965) are known to eat large seastars, but only one record of predation on *A. scabra* exists (Godfriaux, 1969).

SECTION 3

CHAPTER 3. REPRODUCTIVE PERIODICITY AND SOME FACTORS AFFECTING GONAD PRODUCTION IN *ASTROSTOLE SCABRA*

INTRODUCTION

Apart from Crump's (1971) account of reproductive periodicity in *Patiriella regularis*, little substantial information has been published on the reproductive habits of New Zealand seastars. Bennett (1927) reported that autotomous reproduction occurred in *Allostichaster insignis*, *A. polyplax* and *Coscinasterias calamaria*, and Emson (1978) described the process of fission in *A. polyplax*. Fell (1959) noted the brooding habit of *Calvasterias suteri*.

Sexual maturity in some seastar species depends on size (Mead, 1900; MacGintie and MacGintie, 1949) whereas in others gonad production is independent of size or age (Vevers, 1949). Many authors have suggested that reproductive potential in seastars is linked directly to the abundance and type of available food (Vevers, 1949; Pearse, 1965, 1969; Feder, 1970; Birkeland, 1974) and Crump (1971) proved this dependence experimentally in *P. regularis*. An inverse relationship between the size of gonads and pyloric caeca in *Pisaster ochraceous* and *P. brevispinus*, discovered by Farmanfarmaian *et al.* (1958), is related to seasonal feeding patterns as food reserves are stored in the pyloric caeca before transfer to the developing gonads (Anderson, 1953; Mauzey, 1966). The predominant reproductive mode in asteroids is the liberation of gametes into the water and these typically small eggs develop into planktotrophic larvae (Feder and Christensen, 1966). Most starfish have a fairly restricted spawning season (Boolootian, 1966), although three

asterinids, *Patiria miniata*, *Patiriella vivipara* and *P. exigua* have the potential to breed throughout the year (Farmanfarmaian *et al.*, 1958; Dartnall, 1969c; Lawson-Kerr and Anderson, 1978).

Little is known about the reproductive biology of *Astrostole scabra*. Maxwell (1957) obtained fertilisable gametes from specimens in the Wellington region in October 1954 and raised the larvae through to the pelagic bipinnaria stage.

The aims of this study were to determine the annual reproductive cycle in *A. scabra* and to discover if any seasonal relationship existed between the size of gonads and pyloric caeca.

MATERIALS AND METHODS

A minimum of 25 *A. scabra* was collected at monthly intervals from the intertidal and sublittoral locations described in Chapters 2 and 4 from 19 August 1975 to 22 October 1976; more extensive samples were taken throughout August and September 1977. As only subtidal *A. scabra* are fully mature (Chapter 2), these alone were used in the determination of the reproductive cycle, and at least 20 specimens from each monthly sample were obtained from depths of 20-146m.

In the laboratory, the radius of each specimen was measured and a slit made along the abactinal mid-line of each ray to allow removal of gonads and pyloric caeca. The eviscerated body was then drained, blotted and weighed. The displacement volume of gonads and pyloric caeca, drained of surface moisture, was measured separately in a graduated measuring cylinder. Gonad and pyloric caeca indices were calculated according to Farmanfarmaian *et al.* (1958) and Pearse (1965). The ratio of organ volume to eviscerated body weight X 100 was taken as the organ index. The specific gravity of gonads and pyloric caeca did not differ significantly from that of water so conversion to weight was unnecessary.

Each of the fourteen lobulate gonads, two in each arm, had a separate gonoduct and was situated laterally alongisde the ambulacral groove and below the pyloric caeca. The sexes could not be distinguished externally, but from March to August ovaries were bright orange and testes creamy-white. Between September and February smear preparations of dissected gonads were examined microscopically and the presence of oocytes or motile spermatozoa was noted.

Spawning was considered to have occurred when a sharp drop in gonad indices was noted.

RESULTS

Annual reproductive cycle

Gonad sampling commenced in August 1975 and coincided with the peak of gonad development in that year (mean gonad index 10.1). In 1975, spawning occurred between 19 August and 6 September and by the latter point gonad indices had dropped sharply (Fig. 3.1) and all seastars had small, shrunken gonads. This condition persisted until December, when nearly all remaining gonadal tissue had been resorped (mean gonad index 0.3). In 1976, gametogenesis (the appearance of new gonadal tissue), commenced in February-March and gonad indices rose gradually until early May. From early May until early June gonad indices rose rapidly and thereafter only a further slight increase was detected (June mean gonad index 13.5; July mean gonad index 15.8; August mean gonad index 15.2). Ova from dissected gonads were checked for fertilisability from March onwards, but successful fertilisations occurred only in June, July and August. In 1976, *A. scabra* spawned between 28 August and 23 September. Natural spawning was not observed, but the rapid fall in gonad indices suggested that spawning was synchronous and complete. In 1977, spawning occurred between 25 August

FIGURE 3.1: Mean monthly gonad (O) and pyloric caeca (□) indices with 95% confidence intervals for combined male and female *A. scabra* collected from 20-146m at Kaikoura.

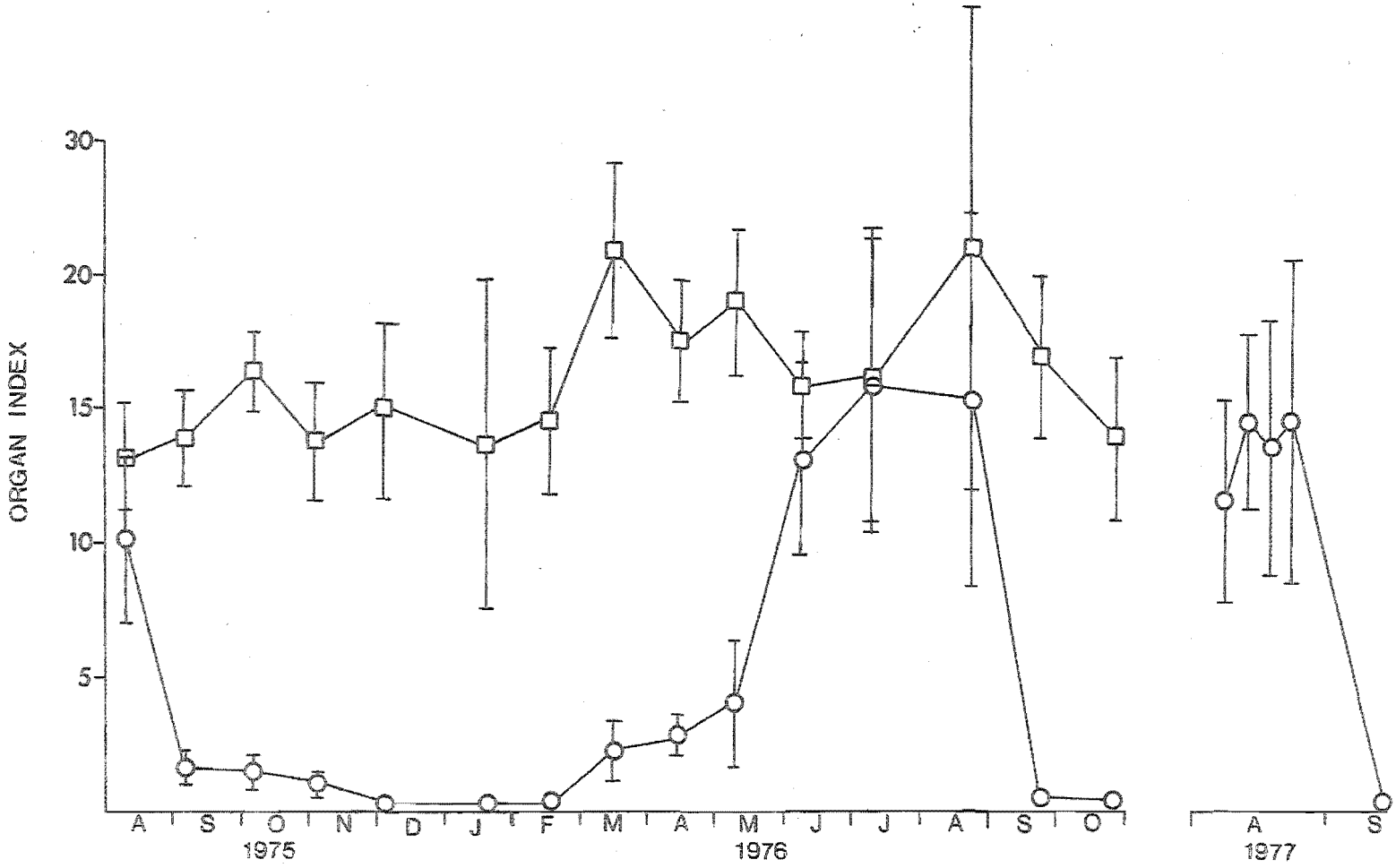
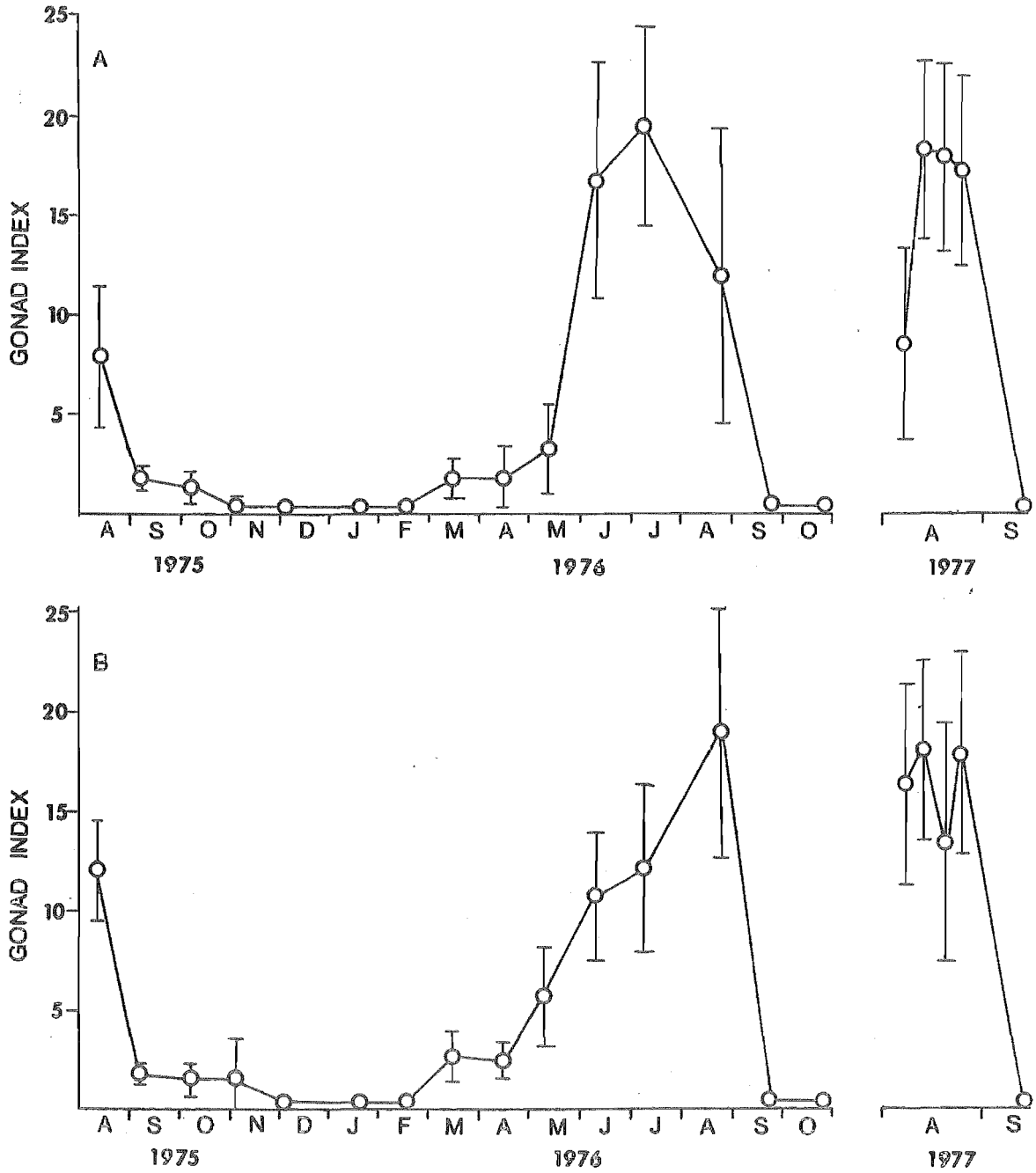

ORGAN INDEX
30
20
15
10
5
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
1975
1976
A
S
1977

FIGURE 3.2: Mean gonad indices with 95% confidence intervals for male (A, n = 217) and female (B, n = 264) *A. scabra* collected from 20-146m at Kaikoura.


A
B
GONAD INDEX
25
20
15
10
5
A S O N D J F M A M J J A S O
1975
1976
A S
1977

and 14 September. During the three years of study, spawning therefore occurred over the same short period from late August - early September. Thus, subtidal (R $\geq$110mm) *A. scabra* have a well defined reproductive cycle and spawn once per year in late winter - early spring.

Annual gonad index cycles were similar for both males and females with some slight differences in detail (Fig. 3.2). In 1976, mean female gonad indices rose gradually from March onwards reaching a peak of 19 in late August. Mean male gonad indices also rose gradually from March, but rose rapidly from May to June. The decline in mean male gonad index detected between early July and late August was caused by sample variation, and there was no evidence to suggest that males spawned in advance of females.

Pyloric caeca indices

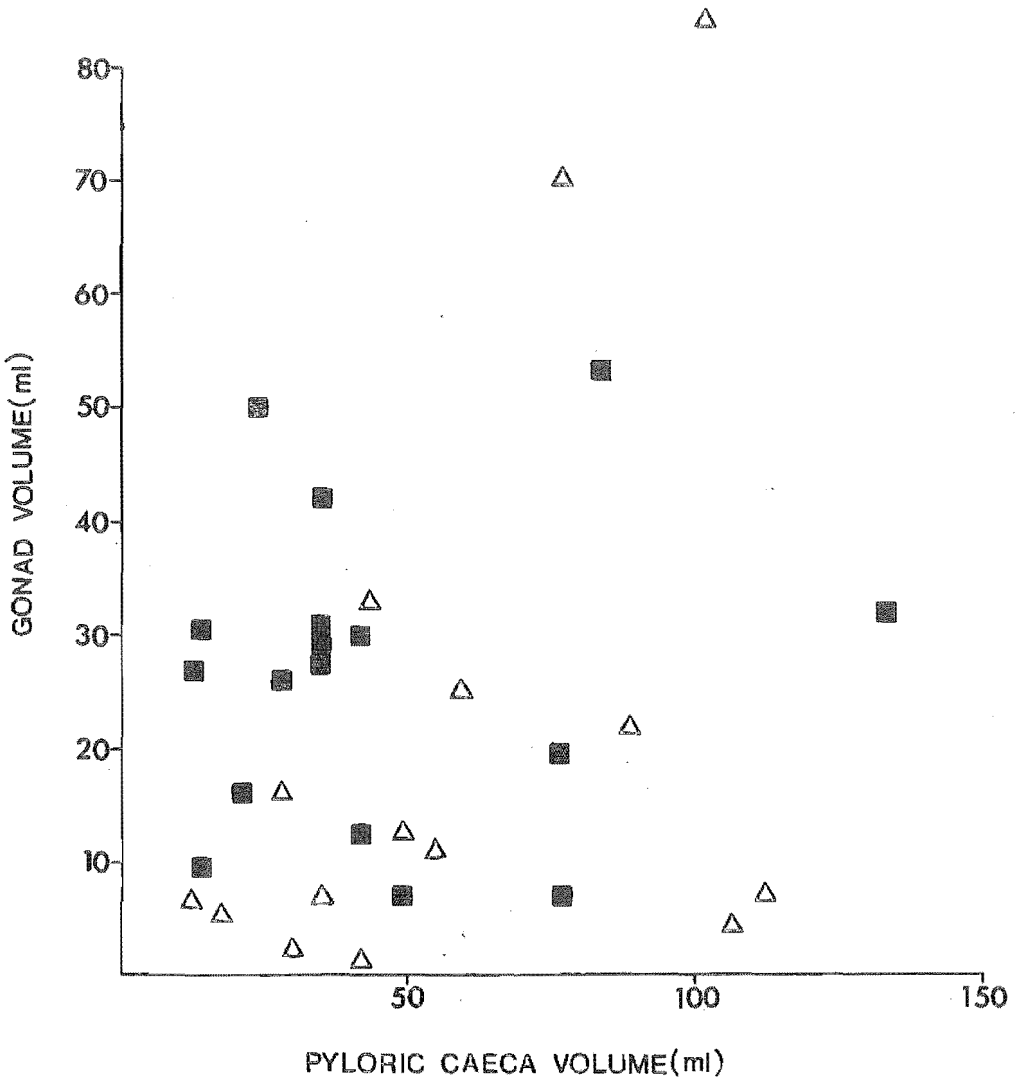
Although mean pyloric caeca indices varied from month to month, there was little direct correlation with gonad indices. Mean pyloric caeca indices did decline slightly during the May-June 1976 period of rapid gonad elaboration, and also during the two months following spawning (Fig. 3.1). This lack of correlation was also evident in individual seastars. In neither male, female, intertidal or sublittoral specimens was there any clear relationship between gonad and pyloric caeca volumes (Figs 3.3, 3.4).

Gonad production

Three factors were found to influence the volume of gonad produced by individual seastars. First, only *A. scabra* of R $\geq$110mm had measurable gonad volumes and in intact, subtidal *A. scabra* of R $\geq$110mm the volume of gonad produced by August was significantly correlated with eviscerated wet weight (Figs 3.5, 3.6). This relationship was identical for both males and females (ANCOVA on slope of regression lines in Figs 3.5 and 3.6, $F = 0.0005$, $0.05 < p < 0.93$). Second, subtidal

FIGURE 3.3: Relationship between female gonad and pyloric caeca volume in subtidal (■) and intertidal (△) *A. scabra* collected at Kaikoura in August 1976.

FIGURE 3.4: Relationship between male gonad and pyloric caeca volume in subtidal (■) and intertidal (△) *A. scabra* collected at Kaikoura in August 1976.


GONAD VOLUME(ml)
80
70
60
50
40
30
20
10
50
100
150
PYLORIC CAECA VOLUME(ml)

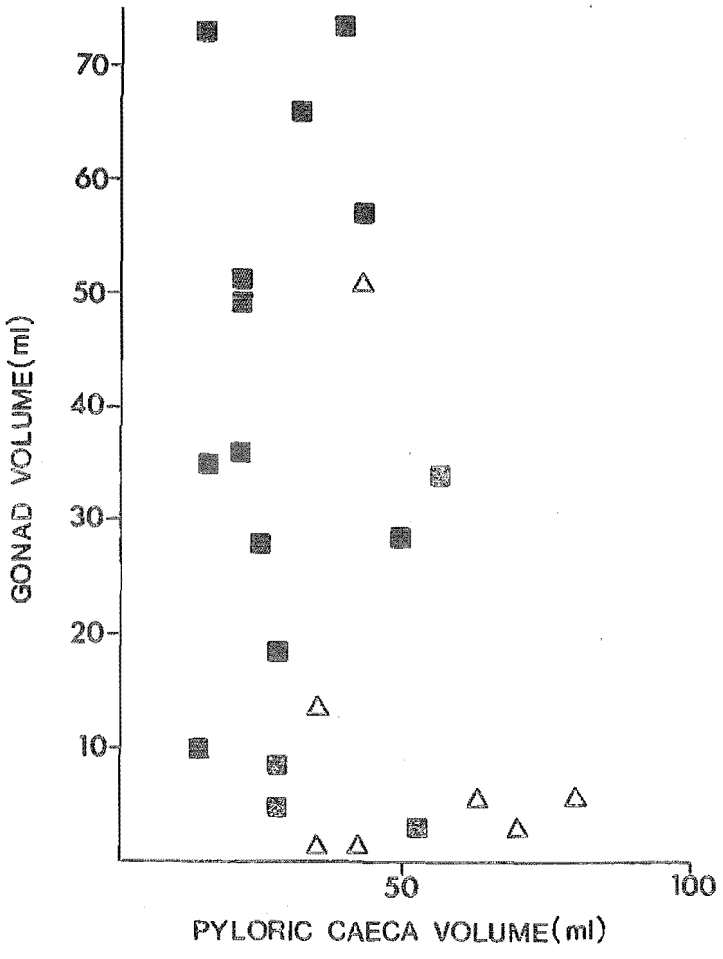
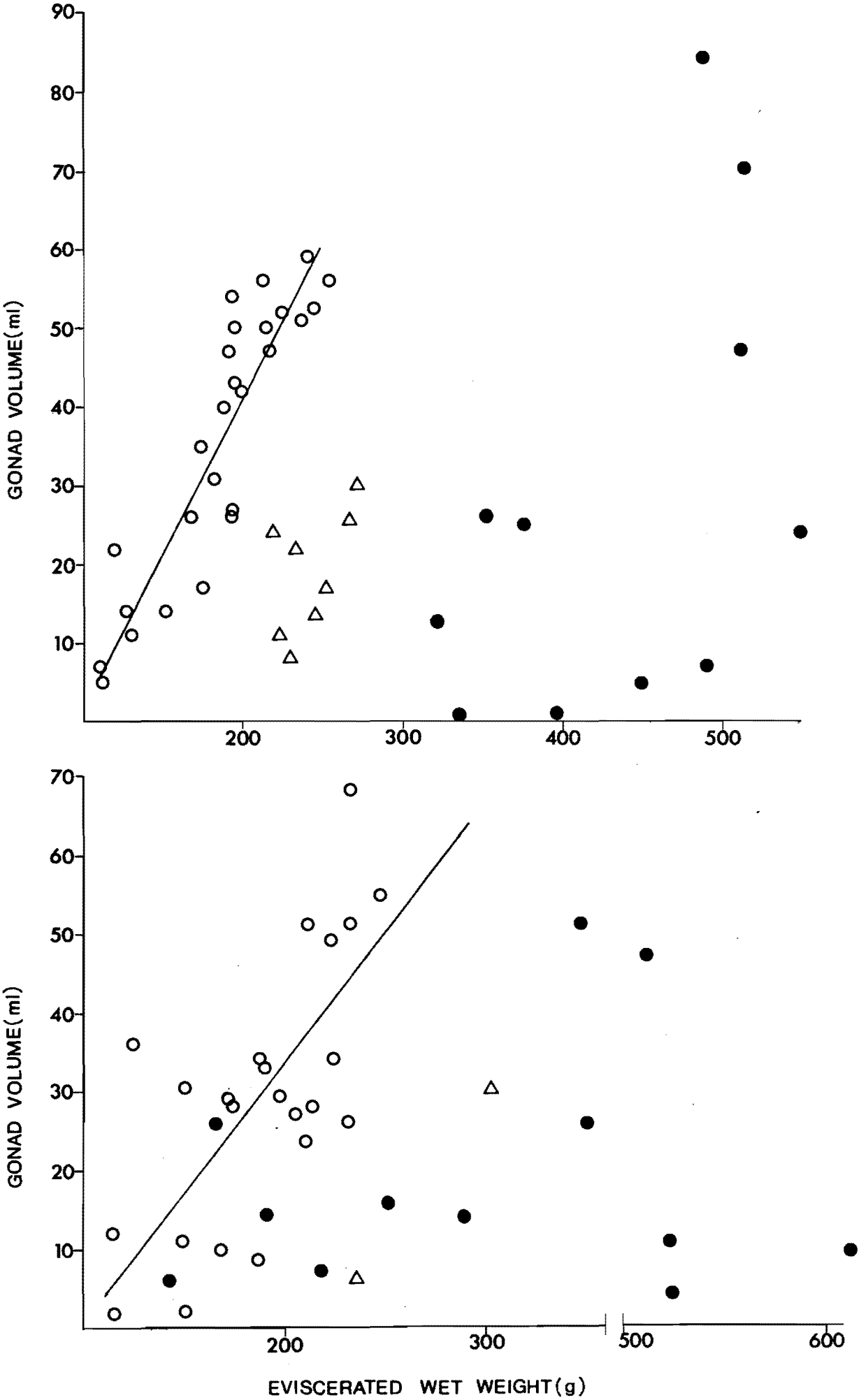

GONAD VOLUME(ml)
70
60
50
40
30
20
10
50
100
PYLORIC CAECA VOLUME(ml)

FIGURE 3.5: Relationship between gonad volume and wet weight of eviscerated body in intact subtidal (○), regenerating subtidal (△), and intact intertidal (●) female *A. scabra* collected at Kaikoura in August 1976. Regression equation: $Y = 0.385X - 35.472$, $n = 26$, $r = 0.896$, $p < 0.005$.

FIGURE 3.6: Relationship between gonad volume and wet weight of eviscerated body in intact subtidal (○), regenerating subtidal (△), and intact intertidal (●) male *A. scabra* collected at Kaikoura in August 1976. Regression equation: $Y = 0.324X - 31.716$, $n = 23$, $r = 0.683$, $p < 0.01$.


GONAD VOLUME(ml)
90
80
70
60
50
40
30
20
10
200
300
400
500
GONAD VOLUME(ml)
70
60
50
40
30
20
10
200
300
500
600
EVISCERATED WET WEIGHT(g)

A. scabra which were regenerating damaged rays in August had lower gonad volumes than their intact counterparts and third, large, thick-skeletoned intertidal seastars had much reduced gonad volumes (Figs 3.5, 3.6).

Sex ratio

The sex ratio of adults collected during the course of the study did not differ significantly from 1:1 (Ratio female : male = 1.21 : 1, $n = 481$, $x^2 = 2.21$, $p > 0.05$).

There was no evidence of hermaphroditism or asexual reproduction.

DISCUSSION

Giese (1959) considered that environmental influences which induce gametogenesis and gamete maturation must act for a more prolonged period than those which trigger spawning. One of the most obvious seasonally variable environmental factors in shallow temperate waters is temperature which, at Kaikoura, rises from October and peaks in January-February (Bradford, 1972). However, Bradford (1972) found no pronounced seasonal temperature variations in waters deeper than 100m off Kaikoura, and most mature seastars were collected from 20-146m. Although Orton (1920) and Kinne (1963) were of the opinion that temperature controlled the time of spawning in most marine animals once certain prerequisites were met, the latter authority warned that organisms react to their total environment and that a monofactorial approach may lead to ecologically invalid conclusions. Mature *A. scabra* were found predominantly at depths of 20-146m off Kaikoura (Chapter 2) and it is improbable that temperature alone initiates spawning and gametogenesis. This view is supported by two further observations; the poles and tropics are generally regarded as stenothermal, yet in Great Barrier Reef waters *Acanthaster planci* has short, well-defined gametogenic and spawning periods (Endean, 1969; Lucas, 1973) and in

Antarctic seas *Odontaster validus* spawns only in winter (Pearse, 1965). The parameters controlling these reproductive events remain undetermined.

Giese (1959) concluded that factors which caused spawning were quite different from those which induced gametogenesis but Mileikovsky (1968) discovered three "physiological races" of *Asterias rubens* distinguished by the temperature at which spawning commenced. Chia (1968) suggested that some "internal stimulus" induced spawning in *Leptasterias hexactis* but Mauzey (1966) postulated that plankton richness ultimately set the timing of reproduction in *Pisaster ochraceous* and Pearse (1965) noted that planktotrophic larval stages of *O. validus* appeared concurrently with annual phytoplankton blooms. Results obtained by Himmelman (1975) are relevant in this regard. He discovered that spawning in the echinoid *Strongylocentrotus droebrachiensis* was caused and synchronised indirectly by the spring phytoplankton bloom and he considered that a compound bound to or released by phytoplankton sensitized the echinoid so that spawning was provoked by slight disturbances. Chaet (1967) discovered that spawning in seastars is the result of a balance between two neurohormones concentrated in the soma of the radial nerves; "shedding substance" and "shedhibin" which inhibits spawning. "Shedhibin" peaked in concentration just prior to spawning and disappeared during or after spawning. Kanatani and Shirai (1968) demonstrated that "shedding substance" did not act as a pheromone. It is feasible that compounds emanating from phytoplankton blooms could cause the observed decline in "shedhibin" levels and thereby cause spawning. Unfortunately, such a mechanism does not explain reproductive periodicity in *Patiriella regularis*, the commonest asteroid of shallow New Zealand waters, which has planktotrophic larvae (Lawson-Kerr and Anderson, 1978) but spawns in mid-summer (Crump, 1971). Nevertheless, studies aimed at detecting any influence of phytoplankton on "shedhibin" concentrations might prove

fruitful.

A. scabra spawned over the same short interval in each of the three years studied (Fig. 3.1). Spawning in late August - early September is coincident with the spring phytoplankton bloom at Kaikoura which, in the only study conducted in the region (Bradford, 1972), occurred at that time. Logically, asteroids which produce large numbers of planktotrophic larvae should spawn when plankton richness is at a maximum and thereby ensure an adequate food supply for their offspring. The question arises as to whether spawning is timed by phsical or biotic exogenous environmental factors or by a purely endogenous rhythm. Natural selection will certainly have favoured those genotypes which spawned at a time most favourable for larval survival, and could act by selecting in favour of particular endogenous rhythms. It is notable that few workers have been able to isolate environmental factors which unquestionably initiate spawning and Mileikovsky's (1968) "physiological races" of *Asterias rubens* might also be separable on the basis of local differences in primary production. Mature, fertilisable ova were present in the ovaries of *A. scabra* from June onwards and female gonad indices did not alter markedly between then and late August (Fig. 3.2). It is a moot point whether seastars were awaiting an environmental signal or the completion of an endogenous rhythm before spawning. Temperature change cannot be invoked as an environmental cue as even the shallowest waters in the Kaikoura region undergo relatively little temperature change between late August and early September (Ottaway, 1976).

Mauzey (1966) noted that arm space occupied by pyloric caeca cannot accommodate gonad, and he suggested that the inverse relationship between pyloric caeca and gonad indices in *P. ochraceous* allowed the release of a maximum number of gametes. He did not, however, investigate this relationship in individual seastars but he did concede that this situation was shown only generally. Mean pyloric caeca indices in

A. scabra did decline during the May-June 1976 period of gonad growth (Fig. 3.1) but by August 1976 no correlation existed between pyloric caeca and gonad volume in individual seastars. Mature *A. scabra* did not cease feeding in either immediate pre- or post-spawning periods, and changes in pyloric caeca indices cannot be attributed to such effects. It should be noted that mature *P. ochraceous* are usually confined to the intertidal zone and show pronounced seasonality in feeding activity (Mauzey, 1966). In contrast, mature *A. scabra* are almost exclusively restricted to depths of 20-146m (Chapter 2) and are not likely to have temperature-inhibited feeding in winter, and thus show seasonally variable pyloric caeca indices. Similarly, *P. giganteus*, a species restricted normally to subtidal situations, had no seasonally inverse correlation between organ indices (Farmanfarmaian *et al.*, 1958). The pronounced seasonality in feeding of intertidal *A. scabra* (Chapter 4) may promote immaturity in these individuals.

Absolute gonad volume in intact, subtidal *A. scabra* appeared to be limited by body size (Figs 3.5, 3.6) and the metabolic requirements of increased body size must be more than offset by enhanced food capture capabilities. The peculiar phenomenon whereby regeneration precludes maximum gonad production (Figs 3.5, 3.6) has not been recorded previously for seastars except perhaps in fissiparous species (Crozier, 1920). Regeneration and gametogenesis might be mutually inhibitory, or the allocation of a portion of energy intake into regeneration may result in the production of fewer gametes. In any case, it is evident that the predominantly subtidal habit of *A. scabra* of R $\geq$110mm is advantageous in terms of gamete production because the incidence of damage is reduced (Chapter 2).

Exactly why *A. scabra* does not develop gonads until R$\geq$110mm is unclear. Barker (1977a) discovered similar size-dependent maturity in *Stichaster australis* and *Coscinasterias calamaria* which do not develop

mature gonads until R= 40mm and 45-50mm respectively. Vevers (1949) was unable to find any correlation between size and maturity in *A. rubens* but he did link reproductive potential with available food supplies. Since food-capturing ability in asteroids is improved by increased size (Menge, 1972b) it may be that smaller *A. scabra* are incapable of catching enough food to support growth, self maintenance and gonad production. Intact *A. scabra* of R = 110-365mm do occur intertidally (Chapter 2), but produce relatively small gonads (Figs 3.5, 3.6). This further implies that intertidal food resources are incapable of supporting substantial gonad development and large size.

A result of the bathymetric separation of mature and immature *A. scabra* at Kaikoura (Chapter 2) is that small seastars do not compete for food with their larger conspecifics. Menge (1972a) demonstrated that the presence of large *P. ochraceous* maintained small size in *L. hexactis* which overlapped broadly with respect to diet.

Reproduction in *A. scabra* is "typical" in that gametes are shed freely and fertilization is external. This mode of reproduction has great potential dispersal powers which can reduce local intraspecific competition and allows the rapid location and colonisation of food-rich areas. These are important selective agents for large seastars (Menge, 1975).

SECTION 4

CHAPTER 4. DIETARY COMPOSITION AND SEASONAL ASPECTS OF FEEDING ACTIVITY IN *ASTROSTOLE SCABRA*

INTRODUCTION

When Feder and Christensen (1966) reviewed the extensive literature pertaining to the feeding habits of seastars, data on dietary composition in 79 species had been amassed. This showed that various feeding methods are used by asteroids and include mud swallowing (Marsden, 1961); muco-ciliary feeding on deposited or suspended particulate organic material (Gemill, 1915; Vevers, 1956; Anderson, 1960; Araki, 1965; Pearse, 1965; B. Rasmussen, 1965; Crump, 1969); grazing on encrusting organisms (Hunt, 1925; Hancock, 1958; Goreau, 1964; Mauzey *et al.*, 1968); utilisation of dissolved exogenous organic material from seawater (Stephens and Schinske, 1961; Ferguson,1964, 1967a, 1967b); and predation on almost any available slow moving or sessile animal (Hyman, 1955). Intensity of feeding activity in temperate zone asteroid populations frequently fluctuates seasonally (Ferguson, 1969; MacKenzie, 1969; Christensen, 1970; Crump and Emson, 1978). In temperate zones, either low winter (Galtsoff and Loosanoff, 1939; Hancock, 1955; Mauzey, 1966; Doi, 1976) or high summer (Hatanaka and Kosaka, 1969) temperatures can suppress feeding. Similarly, in the tropical species *Acanthaster planci*, feeding is reduced by high summer temperatures (Wilson and Marsh, 1974). Storms (Menge, 1972b) and reproductive activity (Hancock, 1955; Chia, 1969; Brun, 1972; Menge, 1972b) may also interrupt feeding. Some studies in temperate zones have shown asteroid feeding activities to be independent of temperature

(Feder, 1970; Martin, 1970; Paul and Feder, 1975).

Dietary composition, which alters with respect to the character of the potential prey community (Mauzey *et al.*, 1968), may also vary seasonally as a result of changed prey abundance (Mauzey *et al.*, 1968; Christensen, 1970; Birkeland, 1974) or predator behaviour (Mauzey, 1966; Kaufman, 1974).

The majority of these data were derived from observations on Northern Hemisphere species. There have been few studies on asteroid feeding in the Southern Hemisphere although the diet of some Antarctic species (Clark, 1963; Dayton *et al.*, 1974; Dearborn, 1977; Kaufman, 1974; Pearse, 1965), and one Chilean species (Dayton *et al.*, 1977) has been investigated. The literature on asteroid feeding biology continues to grow (Brun, 1972; Christensen, 1970; Doi, 1976; Feder, 1970; Hancock, 1974; Lawrence *et al.*, 1974; Mauzey, 1966; Mauzey *et al.*, 1968; Paul and Feder, 1975; Ribi *et al.*, 1977), but more importantly, the ecological implications of these feeding activities have also received recent attention (Birkeland, 1974; Paine, 1966, 1969a, 1969b, 1974, 1976; Dayton, 1971; Dayton *et al.*, 1974; Menge, 1972a, 1972b; Menge and Menge, 1974). These latter studies have shown that the diversity and vertical stratification of some rocky intertidal marine communities is maintained, in part, by asteroid predation.

Substantial unpublished information on the diet of New Zealand asteroids exists. Crump (1969) examined the diet of *Coscinasterias calamaria* and *Patiriella regularis* in Otago Harbour, and Martin (1970) looked at these and another four species, *Stegnaster inflatus*, *Pentagonaster pulchellus*, *Astropecten polyacanthus* and *Stichaster australis*, in the Auckland area. Paine (1971) published an investigation of resource partitioning in a rocky intertidal community at Piha, Auckland, containing the forcipulate, *Stichaster australis*. Dietary data for other local species are restricted to isolated observations

(Bennett, 1927; Fell, 1962b; Grace, 1967, 1974; Morton and Miller, 1973; Young, 1926).

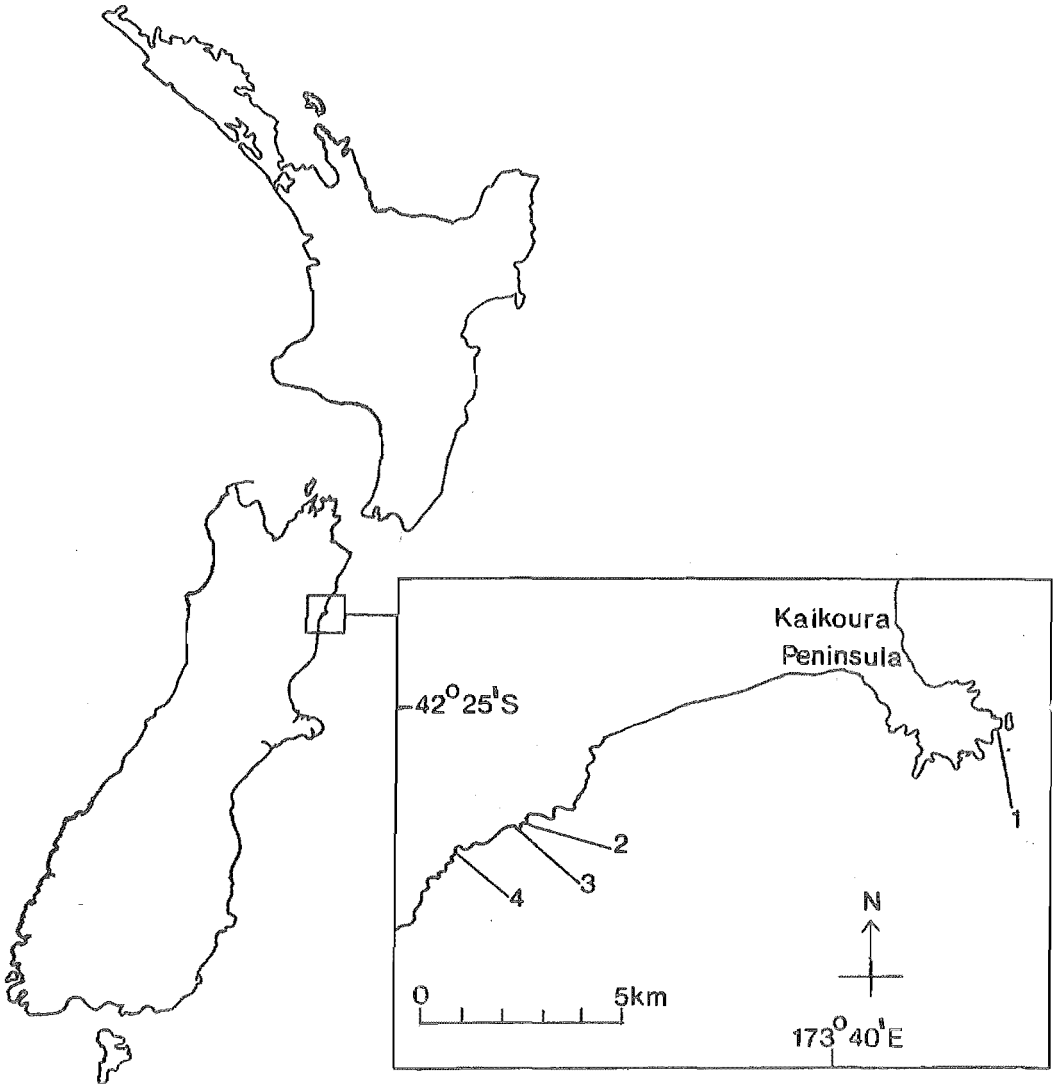
Before the present study, the diet of *Astrostole* was largely unknown. The Easter Island species, *A. paschae*, eats the rock oyster *Chama* sp. and the small gastropod *Nerita morio*. *A. platei* of the Juan Fernandez and Desventuradas Islands consumes small gastropods and mytilids (M. Codoceo, pers. comm.). Fell (1962b) described the diet of *A. scabra* as consisting chiefly of molluscs, and Dix (1969) suspected that the species might be a minor predator of the echinoid *Evechinus chloroticus*. Poore (1969) reported instances of predation on recently dead *Haliotis iris*. Morton and Miller (1973) regarded *A. scabra* as a predator of the holothurian, *Stichopus mollis*. Field and laboratory observations in Tasmania have shown that *A. scabra* feeds on *Haliotis ruber*, *Scutus antipodes*, *Argobuccinium vexillum*, *Pleurobranchus maculatus* and *Paragrapsus gaimardii* (Dartnall, 1969a). In the Wellington region, subtidal *A. scabra* eat *Cantharidus purpuratus*, *Cookia sulcata*, *Eudoxochiton nobilis* and *E. chloroticus* (Dr J. McKoy, pers. comm.). Near Leigh, *A. scabra* feeds almost exclusively on *E. chloroticus* (Dr M. Barker, pers. comm.). *Turbo granosus* is consumed at the Snares Islands and *Trochus viridis* forms part of the species' diet at Open Bay Islands (pers. obs.).

The aims of this study were to observe the feeding behaviour of *A. scabra* in the field and to determine natural dietary composition in four, geographically separated, intertidal sub-populations in the Kaikoura region.

GENERAL STUDY AREA

Feeding activity was monitored at four intertidal sites on the Kaikoura coast (Fig. 4.1). This coast is subject to considerable wave

FIGURE 4.1: Location of four sites used in the feeding study.


Kaikoura
Peninsula
42°25'S
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2
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action, and the sites were selected so as to have similar wave exposure. In storm conditions, at high tide, waves of up to 4m in height may break on the shore (Ottaway, 1977) and move rocks weighing in excess of 50kg considerable distances upshore. At low tide, effects of wave exposure on the intertidal zone are lessened markedly by bedrock outcrops, offlying reefs, and in some instances by extensive stands of bull kelp, *Durvillaea antarctica*. The tides of the region are semidiurnal with a spring tide range of 1.6m (Morgans, 1967) and a neap tide range of approximately 0.8m (N.Z. Tide Tables, Marine Division, Ministry of Transport, Wellington). The interaction of prevailing surface currents and a complex local submarine topography supply the Kaikoura region with cold temperate mixed waters (Knox, 1960). Inshore waters have an annual temperature range of $8.5^{o} - 19.0^{o}C$ (Bradford, 1972; Dix, 1969; Hay, 1977; Ottaway, 1977) and surface water salinity remains between 33.8‰ and 34.6‰ throughout the year (Bradford, 1972), although heavy rainfall can cause localised reduction of salinity. Ottaway (1977) determined that air temperatures in the intertidal zone rarely fall below $3^{o}C$, and normally remain within $1^{o} - 2^{o}C$ of sea temperature, while relative humidities in shaded areas are generally 65-80% and 80-90% during daylight and nocturnal low tides respectively.

STUDY SITES

Site 1, First Bay, on the north-eastern face of Kaikoura Peninsula, is an extensive intertidal platform, developed in Tertiary limestone, overlain at the rear by limestone pebble and cobble storm beaches and hillside deposits (Kirk, 1975). The platform is irregularly traversed by cobble-filled channels and large pools. The cobbles overlie a mixture of coarse sand and pebbles or pebbles alone (Fig. 4.2).

Site 2 is one of many greywacke bedrock shore platforms which form a narrow strip of coastline south of Kaikoura Peninsula. These platforms are deeply dissected and the many indentations and gullies so formed retain water during low tide periods. Many cobbles and boulders, resting on a pebble/coarse sand mixture, lie within these irregularities. This strip of coastline is backed by steep hills which rise to elevations in excess of 300m within 1km of the shore (Kirk, 1975), and consequently shade the area for much of the year (Fig. 4.2).

Site 3, another greywacke shore platform, is closely adjacent to site 2, and is separated from the latter by a large patch of unstable shingle. The Wairere Stream enters the sea across the entervening shingle beach. This site has more loose boulder cover than site 2, and these overlie pebbles. Few, large pools are present (Fig. 4.3). Sites 2 and 3 are the only study sites directly affected by freshwater runoff during periods of heavy rainfall.

Site 4 was the southernmost greywacke shore platform monitored during the study. This bedrock platform is overlain with large, rounded boulders resting on pebbles. This area is bisected by a launching ramp used for rock-lobster boats (Fig. 4.3). Much excess bait is discarded in the area, but animals feeding on this material are not included in the results.

MATERIALS AND METHODS

Between January 1976 and January 1977, each study site was visited at least once monthly at times of low spring tides. During each visit, the same boulders were lifted by hand and their under-surfaces and underlying substrata inspected for *A. scabra*. Specimens were lifted from the rock, and categorised as feeding or non-feeding;

FIGURE 4.2: Site 1, First Bay. An extensive intertidal limestone platform (upper). Site 2, a deeply indented greywacke shore platform (lower).

FIGURE 4.3: Site 3 (upper) and site 4 (lower). Greywacke shore platforms.

an everted stomach was taken as the criterion of feeding. As digestion in *A. scabra* is usually extraoral, prey items were retrieved by gentle teasing of the folds of the everted stomach which withdrew under such treatment. Small prey items were sometimes engulfed whole, but application of gentle pressure to the abactinal surface of the disc caused these to be disgorged. All prey items were preserved in 10% seawater formalin in separate containers, and later identified (where possible) from undigested shells and exoskeletons.

Methods of prey capture in *A. scabra* were observed in the laboratory in a false-bottomed, all-glass aquarium with a mirrored lower surface, supplied continuously with fresh seawater at ambient temperature (9.6 - 18.0°C). This permitted visual inspection of the undersides of feeding seastars. Prey were first allowed to settle on the aquarium bottom before seastars were introduced.

Prey densities at each study site were measured in November 1977, and January and July 1978, by counting all potential prey items occurring within nineteen to thirty-three 0.25 m^2 quadrats placed randomly within areas occupied by seastars. Seastar densities (number of seastars within a known area of shore) were measured monthly at each site from January 1976 to January 1977.

Dietary diversity was measured according to Shannon and Weaver's (1949) open-ended scale:

$$\text{Diversity} = H = -\sum_{i}^{p} pi \log_e pi.$$

pi = the proportion of the ith species in the diet.

Dietary evenness followed Pielou (1966):

$$\text{Evenness} = J = \frac{H}{\log_e S}.$$

S = total number of species in the diet.

J = 1 if predation pressure is exerted equally on all

prey species, and

J = 0 if a single species forms the whole diet.

RESULTS

Feeding behaviour

The intertidal population of *A. scabra* was characteristically composed of small individuals ($R \leq 140$mm) (Chapter 2). These actively foraged when submerged at each high tide period, irrespective of solar rhythm (pers. obs.). Whilst foraging, specimens of *A. scabra* moved across the substratum with one, two or three rays leading. The tips of these leading rays were raised slightly and bent abactinally. The most distal tube feet were spread in the water and waved. Following rays had withdrawn distal tube feet and some reduction in the degree of abactinal flexure of the tips. If food was caught during foraging periods the seastar retreated to the underside of rocks where digestion commenced and continued through the following low tide period. At these times, 90.5% of the starfish population were located beneath rocks, the undersurfaces of which were immersed, 2.0% resided beneath wholly-emersed boulders, and 7.5% remained exposed. Attached molluscs were pulled from the rocky substratum by application of tube feet proximal to the mouth to the mollusc shell. The seastar then raised its disc above the substratum while the tube feet maintained a grip on the prey, and the force applied thus detached the mollusc from the rock. Once prey were separated from the substratum, the seastar assumed a characteristic "humped" position, in which the disc remained elevated. The prey was then applied to the mouth opening and inverted. Captured chitons rolled into a ball, but were "straightened out" simply by the pull of proximal tube feet; alternatively, the cardiac stomach was inserted through a small gap remaining at the axis of curvature between

two shell plates. Haliotids, patellids, acmaeids, pulmonates and fissurellids have no total retreat into skeletal structures, and once prized from the rock were digested easily. Spiral shelled molluscs were pulled from rock surfaces in a manner identical with that used for the capture of chitons. However, these species retreated wholly within their shells, and the operculum was closed to form a seal. In these situations, the seastar adopted one of two procedures to overcome this resistance. Firstly, the operculum was simply pulled off, or secondly, the stomach everted to fill the shell aperture. When the mollusc emerged, it was immediately and unavoidably contacted by folds of the everted stomach and digested.

The skeletal components of echinoderms and crustaceans were not digested, and were discarded once internal tissues had been consumed. The route by which the cardiac stomach gained entry to the inside of intact crustaceans, and the mechanism employed to crush the test of echinoids during digestion are unknown. Isopods were held always with the ventral surface applied to the stomach, and were frequently broken across the mid-lateral axis. Whether this was effected by tube feet prior to, or occurred as a consequence of digestion was not determined. Many prey species such as isopods, fish and crabs are relatively active organisms. However, the application of these food items to pedicellariae of *A. scabra* failed to demonstrate that the latter play a role in food capture. The exact method of capture of active prey remains to be studied.

Digestion did not always immediately follow prey capture. In aquaria, foraging was seen to continue while captured prey was held in position by tube feet approximately half way along a ray.

Overall dietary composition

Of 2581 *A. scabra* inspected during the survey period, 773

(29.94%) were feeding on 938 prey items. The prey data are presented in Table 4.1, and indicate that the seastar is a food generalist and a scavenger. The diet was composed chiefly of molluscs (68.05%) and crustaceans (10.89%), belonging to more than 60 genera. However, a large portion (15.49%) was comprised of unidentified species from everted stomachs. The latter included instances when the stomach was everted over a variety of encrusting organisms, but in none of these cases were signs of digestion present. Further records within this category included eversion of the stomach on to apparently barren rock, and in one case into a substratum of coarse sand. These specimens may have been utilising detritus, as demonstrated by Mauzey (1966) for *Pisaster ochraceus*.

Frequently, moribund or dead organisms were eaten. A number of records fall into this category, and include (with numbers in parentheses), *Eudoxochiton nobilis* (1), *Haliotis iris* (1), *Scutus breviculus* (1), *Turbo smaragdus* (6), *Notopaphia elegans* (1), *Octopus maorum* (1), Squid (1), *Tessarabrachion oculatum* (3), *Plagusia chabrus* (5), *Petrolisthes elongatus* (1), *Myctophum humboldti* (2), and fish carcasses (3). All records of predation on the large crab, *Plagusia chabrus*, were of dead specimens, and in one instance, a single carcass was consumed simultaneously by eight *Patiriella regularis* and one *A. scabra*.

The diet was dominated numerically by trochids (18.91%) and chitons (16.98%). Other molluscan prey included rissoids (7.69%), turbinids (6.08%) and littorinids (4.48%). Of the trochids, *Micrelenchus dilatatus* was the most important, and formed 49.71% of all records of predation on members of this group, and 13.7% of all prey molluscs. *Melagraphia aethiops* was the second most important prey trochid and accounted for 34.46% of records. Prey chitons were predominantly *Ischnochiton maorianus* which represented 52.2% of all

TABLE 4.1. List of prey species and their frequency (%) in the diet of 773 feeding individuals of *A. scabra* examined at four different study sites in the Kaikoura region between January 1976 and January 1977.

PREY SPECIES	SITE 1	%	2	%	3	%	4	%	TOTAL	%
Phylum Porifera										
Tethya aurantium	1	0.28							1	0.1
Phylum Annelida										
Class Polychaeta										
Spirorbis borealis	14	3.93	4	2.2	3	1.45	2	1.03	23	2.45
Phylum Mollusca										
Class Polyplacophora										
Ischnochiton maorianus	31	8.7	21	11.6	18	8.73	13	6.73	83	8.84
Onithochiton neglectus	4	1.12	7	3.86	10	4.85	9	4.66	30	3.19
Amaurochiton glaucus	2	0.56	6	3.31	4	1.94	16	8.29	28	2.98
Sypharochiton pelliserpentis	8	2.24			1	0.48			9	0.93
Eudoxochiton nobilis			1	0.55			2	1.03	3	0.31
Acanthochiton zelandicus			1	0.55			1	0.51	2	0.21
Guildingia obtecta							1	0.51	1	0.1
Chiton (indet.)	1	0.28			1	0.48	1	0.51	3	0.3
Class Gastropoda										
Family Haliotidae										
Haliotis iris	5	1.4	2	1.1	1	0.48	3	1.55	11	1.17
H. australis							1	0.51	1	0.1
Family Patellidae										
Cellana radians	2	0.56	5	2.76	4	1.94	9	4.66	20	2.13
C. ornata	1	0.28							1	0.1
C. denticulata	1	0.28	1	0.55	1	0.48	2	1.03	5	0.53
Family Acmaeidae										
Patelloida corticata	2	0.56	1	0.55	2	0.97	5	2.59	10	1.06
Family Fissurellidae										
Scutus breviculus			1	0.55					1	0.1
Family Rissoidae										
Eatoniella sp.	19	5.33	6	3.31	5	2.42	12	6.21	42	4.47
Estea sp.	5	1.4	3	1.65	2	0.97	9	4.66	19	2.02
Rissoina chathamensis	3	0.84	3	1.65	3	1.45	2	1.03	11	1.17
Family Cerithiidae										
Zeacumantus sp.	7	1.96			2	0.97			9	0.95
Family Littorinidae										
Risellopsis varia	7	1.96			20	9.7	15	7.77	42	4.47
Littorina unifasciata					1	0.48			1	0.1
Family Trochidea										
Melagraphia aethiops	27	7.58	15	8.28	11	5.35	8	4.14	61	6.5
Micrelenchus dilatatus	10	2.8	41	22.6	25	12.1	12	6.21	88	9.38
Cantharidella tessellata	8	2.24	7	3.86	8	3.88	3	1.55	26	2.77
Anisolidoma lugubris	1	0.28			1	0.48			2	0.21
Trochids (indet.)	2	0.56							2	0.21
Family Turbinidae										
Turbo smaragdus	51	14.3	1	0.55	3	1.45	2	1.03	57	6.07
Family Cominellidae										
Cominella maculosa	4	1.12							4	0.42
C. glandiformis	4	1.12	2	1.1	2	0.97	3	1.55	11	1.17
Cominella sp.					1	0.48			1	0.1
Family Buccinulidae										
Buccinulum vitatum	2	0.56			1	0.48			3	0.31
B. bicinctum	1	0.28					1	0.51	2	0.21
Class Pelecypoda										
Aulacomya maoriana	8	2.24	1	0.55	1	0.48	5	2.59	15	1.59
Mytilus edulis	1	0.28			1	0.48			2	0.21
Modiolus zelanicus							1	0.51	1	0.1
Hiatella australis					1	0.48			1	0.1
Protothaca crassicosta	5	1.4	4	2.2	1	0.48			10	1.06
Zearcopagia disculus	1	0.28							1	0.1
Notopaphia elegans	1	0.28							1	0.1
Class Cephalopoda										
Octopus maorum	1	0.28							1	0.1
Squid (indet.)			1	0.55					1	0.1
Sub-class Pulmonata										
Siphonaria zelandica	5	1.4	2	1.1	3	1.45	8	4.14	18	1.91

Table 4.1 (Cont'd)

PREY SPECIES	SITE 1	%	2	%	3	%	4	%	TOTAL #	%
Phylum Arthropoda										
Class Crustacea										
Sub-class Cirripedia										
Chamaesipho brunnea	7	1.96			1	0.48			8	0.85
Elminius plicatus	4	1.12							4	0.42
Mitella spinosa							1	0.51	1	0.1
Order Isopoda										
Exosphaeroma obtusum	6	1.68	7	3.86	17	8.25	4	2.07	34	3.62
Dynamenopsis varicolor					1	0.48			1	0.1
Isopod (indet.)	1	0.28			1	0.48			2	0.21
Order Euphausiacea										
Tessarabrachion oculatum					3	1.45			3	0.31
Order Decapoda										
Petrolisthes elongatus	2	0.56	1	0.55					3	0.31
Elamena producta	6	1.68	3	1.65	2	0.97			11	1.17
Cancer novaezelandiae	3	0.84			1	0.48	1	0.51	5	0.53
Plagusia chabrus	1	0.28			1	0.48	3	1.55	5	0.53
Heterozius rotundifrons							1	0.51	1	0.1
Pagurus novaezelandiae	6	1.68	2	1.1	1	0.48	2	1.03	11	1.17
Notomithrax ursus	2	0.56	3	1.65	1	0.48	1	0.51	7	0.74
N. minor							1	0.51	1	0.1
Notomithrax sp.	1	0.28					2	1.03	3	0.31
Phylum Echinodermata										
Class Echinoidea										
Evechinus chloroticus	1	0.28							1	0.1
Class Ophiuroidea										
Ophionereis fasciata	2	0.56			1	0.48			3	0.31
Class Asteroidea										
Patiriella regularis					1	0.48	1	0.51	2	0.21
Phylum Chordata										
Class Ascidiacea										
Ciona intestinalis			1	0.55	1	0.48			2	0.21
Class Actinopterygii										
Order Acanthopterygii										
Dellichthys morelandi							1	0.51	1	0.1
Myctophum humboldti					2	0.97			2	0.21
Tripterygion sp.	1	0.28							1	0.1
Miscellaneous										
Fish eggs (*Diplocrepis* sp.)	3	0.84	1	0.55			2	1.03	6	0.63
Fish eggs (*Dellichthys*)	1	0.28							1	0.1
Fish carcass					1	0.48	2	1.03	3	0.31
Crustaceans (indet.)	4	1.12	2	1.1					6	0.63
Nudibranch (indet.)							1	0.51	1	0.1
Everted stomach	62	17.4	25	13.8	34	16.5	24	12.4	145	15.45

chiton prey. The isopod, *Exosphaeroma obtusum* represented 37.5% of all crustacean prey.

In the four populations of *A. scabra* studied, *M. dilatatus*, *I. maorianus*, *M. aethiops*, *T. smaragdus*, *Risellopsis varia*, *Eatoniella* sp., *E. obtusum*, *Onithochiton neglectus* and *Amaurochiton glaucus* were the nine numerically most important prey species, and together they constituted 50% of all prey items.

The extremely generalised nature of the diet was emphasised by the fact that *M. dilatatus*, the numerically most important prey species, represented only 9.3% of all prey items. Of all other prey species, only *I. maorianus*, *T. smaragdus* and *M. aethiops* represented more than 5% of prey items. Twenty-two prey species occurred as single records, and four of these were moribund or dead before consumption. Perhaps a more accurate assessment of the importance of a prey species as food is provided by the number of meals composed of only a single specimen of a particular prey. Data presented in Table 4.2 show that *T. smaragdus* achieved the greatest importance as a food species, but *M. dilatatus*, although forming 9.3% of all items, constituted only 6.2% of all meals. Further consideration of the relative nutritional importance of prey species in the diet is presented in Chapters 7 and 8.

Additional records obtained outside the survey period, showed that the diet of subtidal *A. scabra* at Kaikoura included the molluscs *Maurea pellucida*, *Buccinulum bicinctum*, *B. vitatum*, *T. smaragdus* and *Aulacomya maoriana*, and the stalked ascidian *Pyura pachydermatina*. In laboratory aquaria, *A. scabra* accepted almost any food offered, and was observed eating the molluscs *Haustrum haustorium*, *Paphirus largillierti*, *Diloma arida*, *Struthiolaria papulosa*, and the stalked barnacle, *Lepas* sp. The asteroid *Sclerasterias mollis* was also eaten in the laboratory.

Although *A. scabra* does not normally occur above MLWN, I have a few records of predation on organisms normally found higher upshore than

A. scabra. Such food items included *Cellana ornata*, *C. denticulata*, *Sypharochiton pelliserpentis*, *Zeacumantus* sp., and *Mytilus edulis*. It is likely that these species fall prey when dislodged and washed into the lower intertidal.

Comparison of diet between sites

Although the four sub-populations had similar diets, several site-specific differences were apparent (Fig. 4.4). In numerical terms, four different prey hierarchies can be erected for the areas studied, viz:-

Site 1: *T. smaragdus*> *I. maorianus*> *M. aethiops*> *Eatoniella*.

Site 2: *M. dilatatus*> *I. maorianus*> *M. aethiops*> *Cantharidella tessellata*, *O. neglectus*, *E. obtusum*.

Site 3: *M. dilatatus*> *R. varia*> *I. maorianus*> *E. obtusum*.

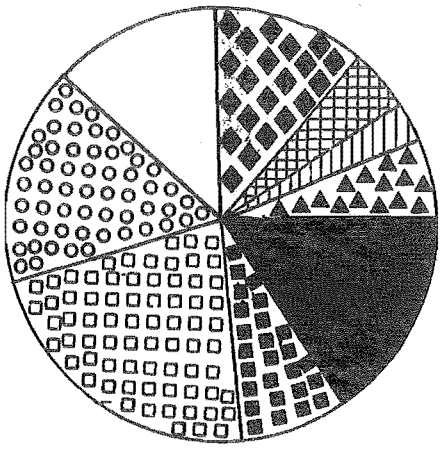
Site 4: *A. glaucus*> *R. varia*> *I. maorianus*> *Eatoniella*, *M. dilatatus*.

These hierarchies indicate that of all prey species, only *I. maorianus* was an important dietary component at all sites. Further, only 21 prey species (29.57% of the total) were common to the diet of seastars at all sites. Although prey density varied at each locality, this factor *per se* did not account for all of the observed intersite differences in dietary composition (Chapter 7). Major differences in diet included almost exclusive predation on *S. pelliserpentis* at site 1, whereas *O. neglectus* and *A. glaucus* were important prey species at other sites. The small rissoid, *Eatoniella* sp. was also a relatively more important dietary component at sites 1 and 4 than at sites 2 and 3. Of a total of 57 records of predation on *T. smaragdus*, 51 were obtained from site 1. This species occurred at all sites. Additionally, bivalves were a minor part of the whole diet, but 50% of all such records were derived from observations at site 1.

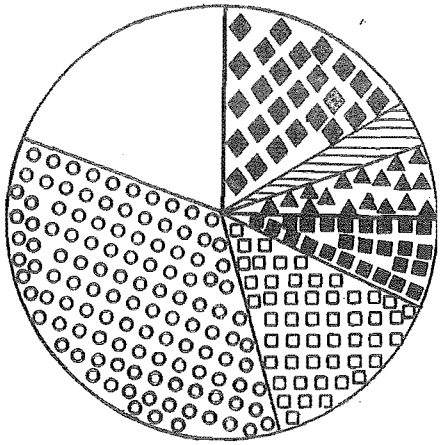
M. dilatatus dominated the diet at sites 2 and 3, but these sites

FIGURE 4.4: Quantitative distribution of prey groups of *A. scabra* from the four study sites. Results from all localities combined as "whole diet" (n = number of starfish examined).

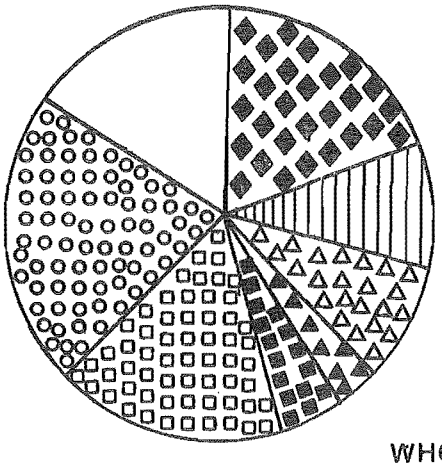
SITE 1
n=313



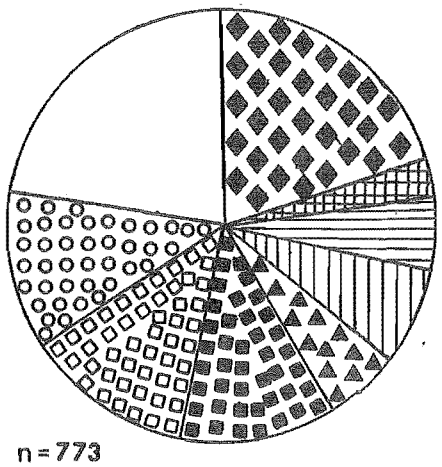
SITE 2
n=139



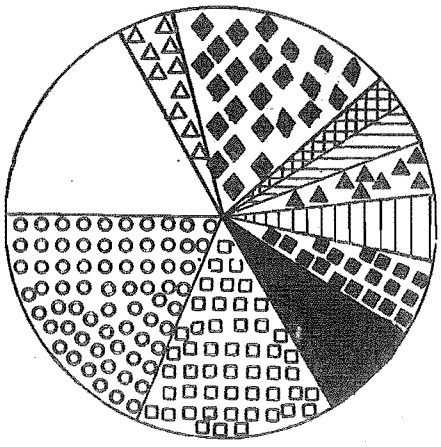
SITE 3
n=172



SITE 4
n=149



WHOLE DIET n=773



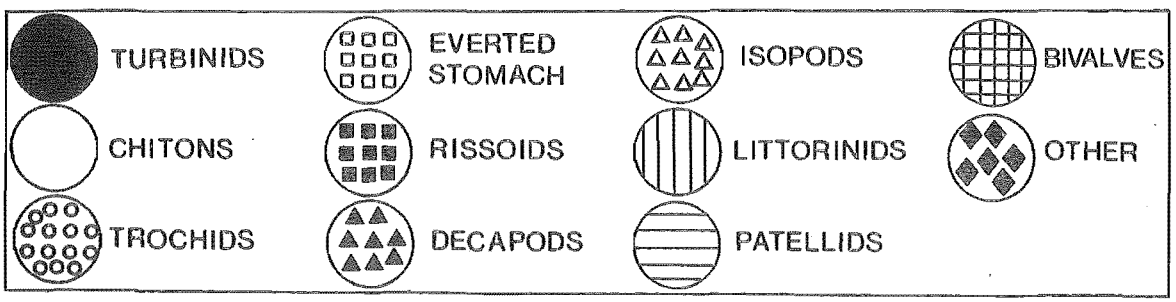


TABLE 4.2. Dietary proportion in total meals of major prey species.

PREY SPECIES	TOTAL NOS. EATEN	TOTAL MEALS OF ONE SPECIMEN	MAX. PREY/MEAL
Ischnochiton maorianus	83	48	4
Amaurochiton glaucus	28	24	1
Onithochiton neglectus	30	24	2
Eatoniella sp.	42	16	6
Risellopsis varia	42	23	4
Melagraphia aethiops	61	40	3
Micrelenchus dilatatus	88	44	4
Turbo smaragdus	57	57	1
Exosphaeroma obtusum	34	15	3

TABLE 4.3. Number of observations and diet characteristics for *A. scabra* at four study sites.

	SITE			
	1	2	3	4
Total site visits	22	19	23	19
Total seastars observed	1115	393	563	510
Total feeding	313	139	172	149
No. prey items	358	181	206	193
Average prey/meal	1.143	1.302	1.197	1.295
Total spp. eaten	52	32	45	41
Mean % feeding	28.07	35.36	30.55	29.21
Range % feeding	52.5-17.15	47.62-9.09	45-14.64	60-15.38
Mean seastars/m^2	0.069	0.072	0.062	0.066
Site area (m^2)	728.8	301.68	380.42	404
H	2.986	2.696	3.306	3.155
J	0.759	0.778	0.868	0.849

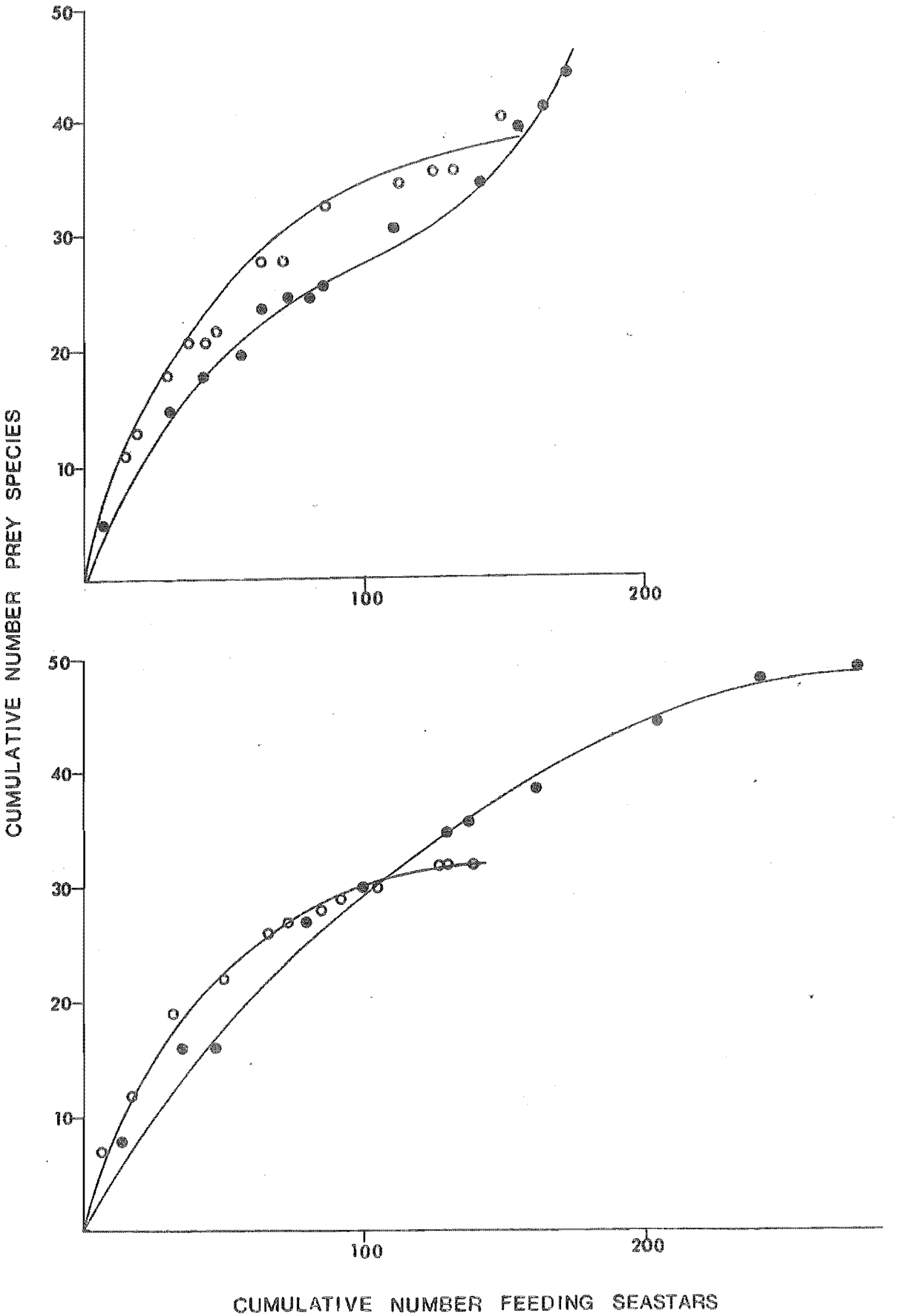
differed markedly in the relative proportions of subsidiary prey species. Most notable was the absence of *R. varia* from the diet of seastars of site 2, whereas at site 3 it constituted almost 10% of prey numbers. In like manner, the isopod *E. obtusum* was eaten more than twice as frequently at site 3 than at site 2.

M. dilatatus (22.6%) and *I. maorianus* (11.6%) at site 2, and *T. smaragdus* (14.3%) at site 1 were the only prey species which constituted more than 10% of prey numbers at any study site.

All sites were broadly comparable in the mean and range proportions of seastars feeding, and in dietary diversity (H) (Table 4.3). Clearly, despite the different proportional basis of diets at each site, dietary diversity (food generality) and evenness were maintained at comparable levels.

Seastars at site 3 had the most diverse and even diet, and animals at site 2 had the least diverse diet. The latter can be attributed to the relatively heavy predation pressure exerted on *M. dilatatus* and *I. maorianus* at this locality. Although the diet of *A. scabra* at site 1 was intermediate in diversity, it was the least even. This was due to the relatively unimportant dietary contributions from *O. neglectus* and *A. glaucus* and the consequent relative predominance of *I. maorianus* and *T. smaragdus*. A large number of "everted stomach" records also contributed toward the reduction of dietary evenness at this site. Full descriptions of overall dietary composition have been obtained for sites 1, 2 and 4 (Fig. 4.5). The cumulative number of species eaten at these sites approaches an asymptote. The sigmoidal curve generated by dietary data from site 3 would probably flatten at a point similar to that evident at site 1, in spite of the fact that the number of seastars inspected at site 3 is only a little over half that of site 1. The reasons behind enhanced dietary diversity at site 3 remain unclear.

FIGURE 4.5: Cumulative number of prey species eaten and cumulative number of feeding seastars at the four study sites.


50
40
30
20
10
100
200
CUMULATIVE NUMBER PREY SPECIES
CUMULATIVE NUMBER FEEDING SEASTARS

Seasonal aspects of feeding behaviour and dietary composition

In addition to the tidal rhythm of foraging activity referred to earlier, there was a distinct annual cycle in the proportion of the intertidal population feeding during each month. The proportion of animals feeding at any one time at any single site fluctuated widely, and this seasonal aspect of feeding was apparent only when data from all four sites were combined (Fig. 4.6). The proportion of the intertidal population feeding reached a peak of 42% in January 1976, and subsequently fell to 23.7% in June 1976. The general pattern was therefore of high summer and low winter feeding activity. The overall annual cycle was disrupted in November 1976 and January 1977 by a pronounced decline in feeding by seastars at sites 2 and 3.

The diversity of the whole diet remained within a narrow range throughout the year (Fig. 4.7), with a minimum of 2.58 (February 1976) and a maximum of 2.99 (October 1976). Similarly, dietary evenness was confined within close limits (minimum 0.808 in September 1976, maximum 0.935 in December 1976). The diversity of diets at each site was closely correlated with the number of seastars feeding (Fig. 4.8), and dietary evenness varied little from month to month. Thus, the diet remained generalised throughout the year, and no single prey species was subjected to seasonally variable predation pressure (Tables 4.4 - 4.7). Some seasonality was suggested by data from single sites. *M. aethiops* was not eaten at site 1 in winter, whereas it achieved peak importance as food for seastars at site 2 at this time. Rissoids were eaten at site 3 only in autumn, but occurred as prey throughout the year at other localities. A single minor food source, eggs of the clingfish, *Diplocrepis*, are laid on the underside of rocks in late winter and early spring and were therefore available and eaten only then. With the exception of one instance, *Pagurus novaezelandiae* was consumed between September and January. Taken in isolation, seasonal data from single

FIGURE 4.6: Seasonal variation in the proportion of animals feeding (upper), and the monthly variation at each site (three lower graphs). Numbers at each point refer to the total number of animals inspected at each site per month.

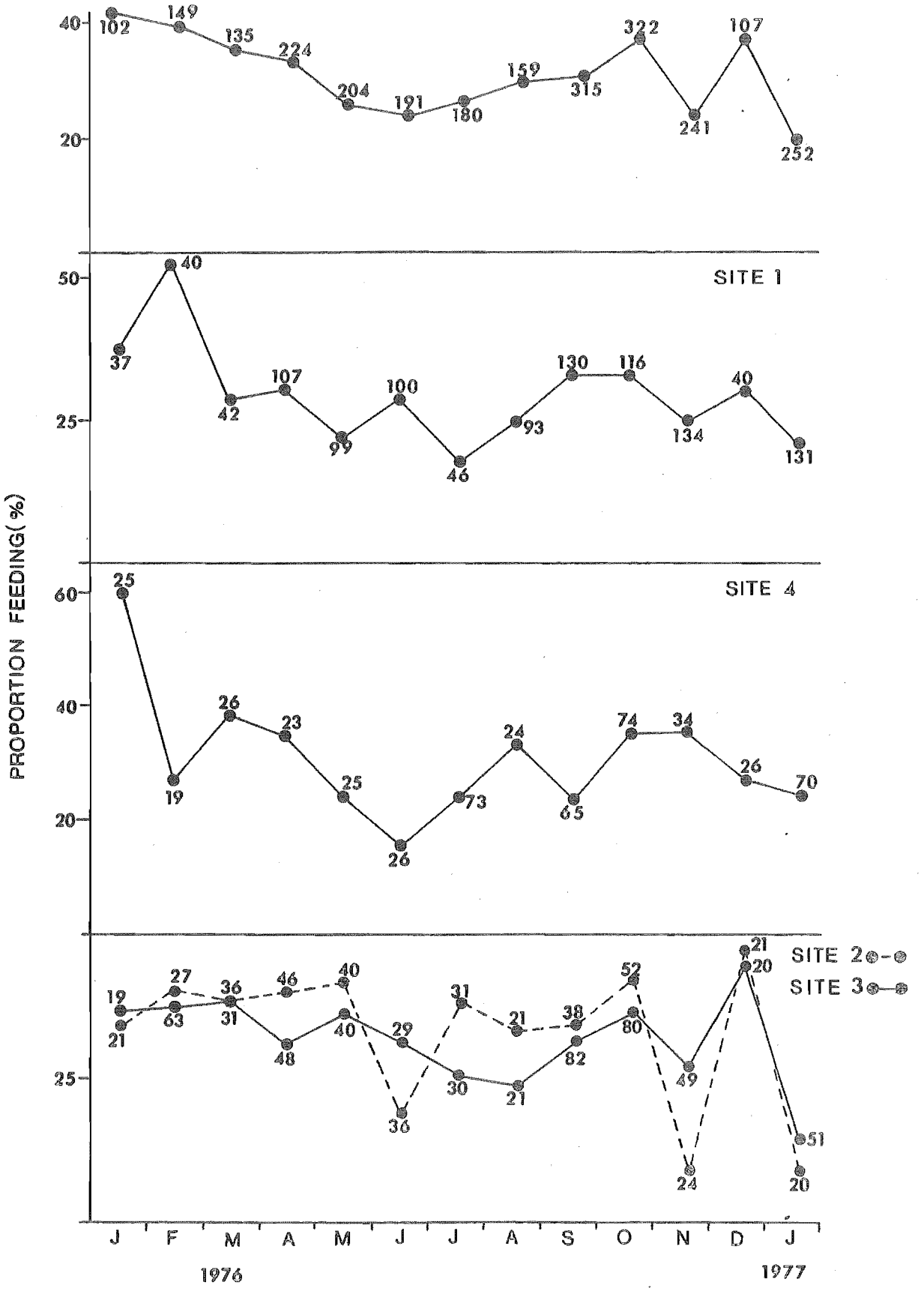

PROPORTION FEEDING(%)
SITE 1
SITE 4
SITE 2
SITE 3
J F M A M J J A S O N D J
1976
1977

FIGURE 4.7: Diversity (H) and evenness (J) of the whole diet throughout the year, compared with the proportion of the seastar population engaged in feeding activity (Δ). (Data from 4 study sites combined.)

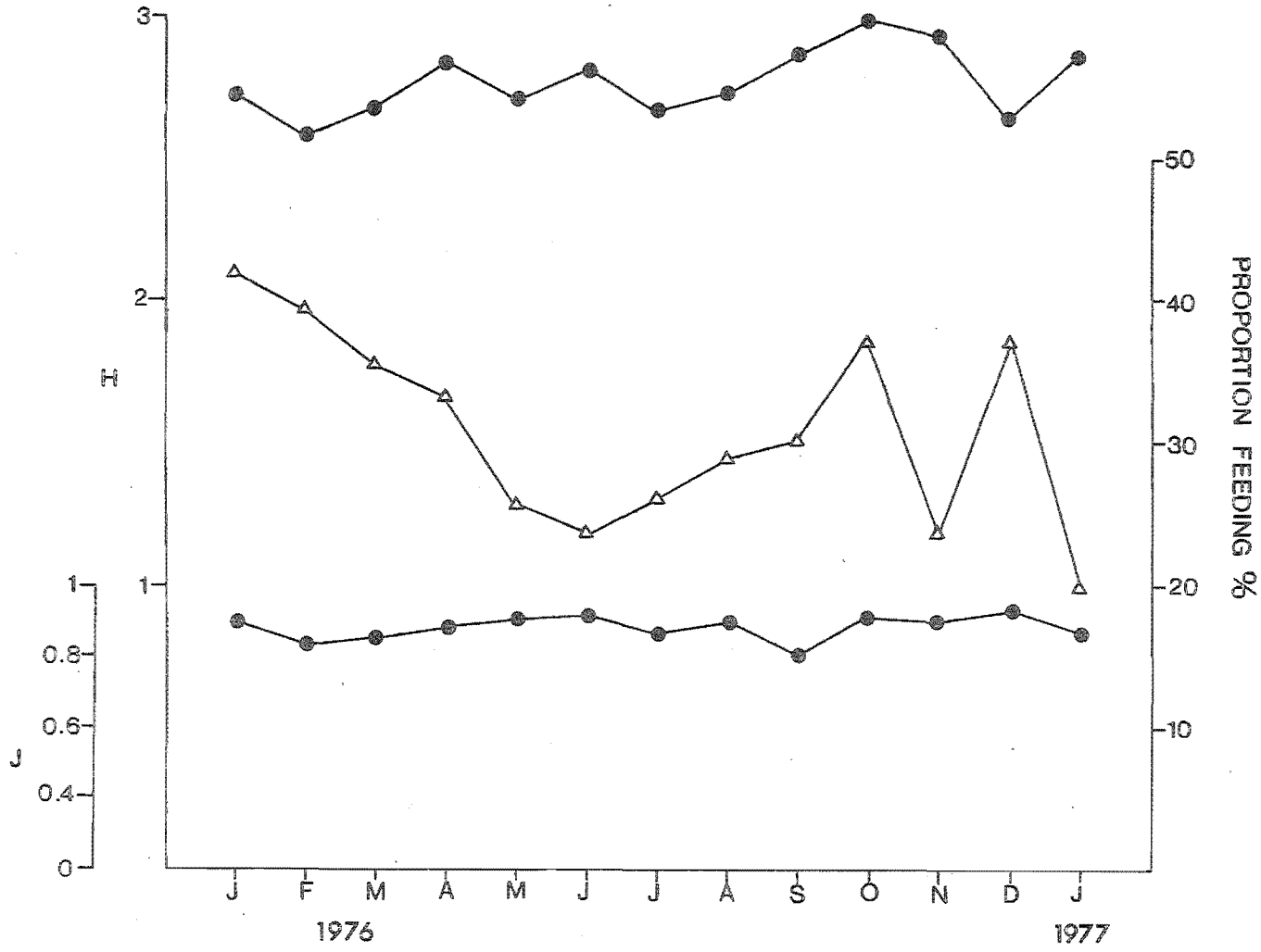

3
2
1
H
1
0.8
0.6
0.4
0
J
50
40
30
20
10
PROPORTION FEEDING %
J F M A M J J A S O N D J
1976
1977

FIGURE 4.8: Number of animals feeding (solid line) and the diversity of the diet (H, pecked line) at sites 1-4 throughout the year.

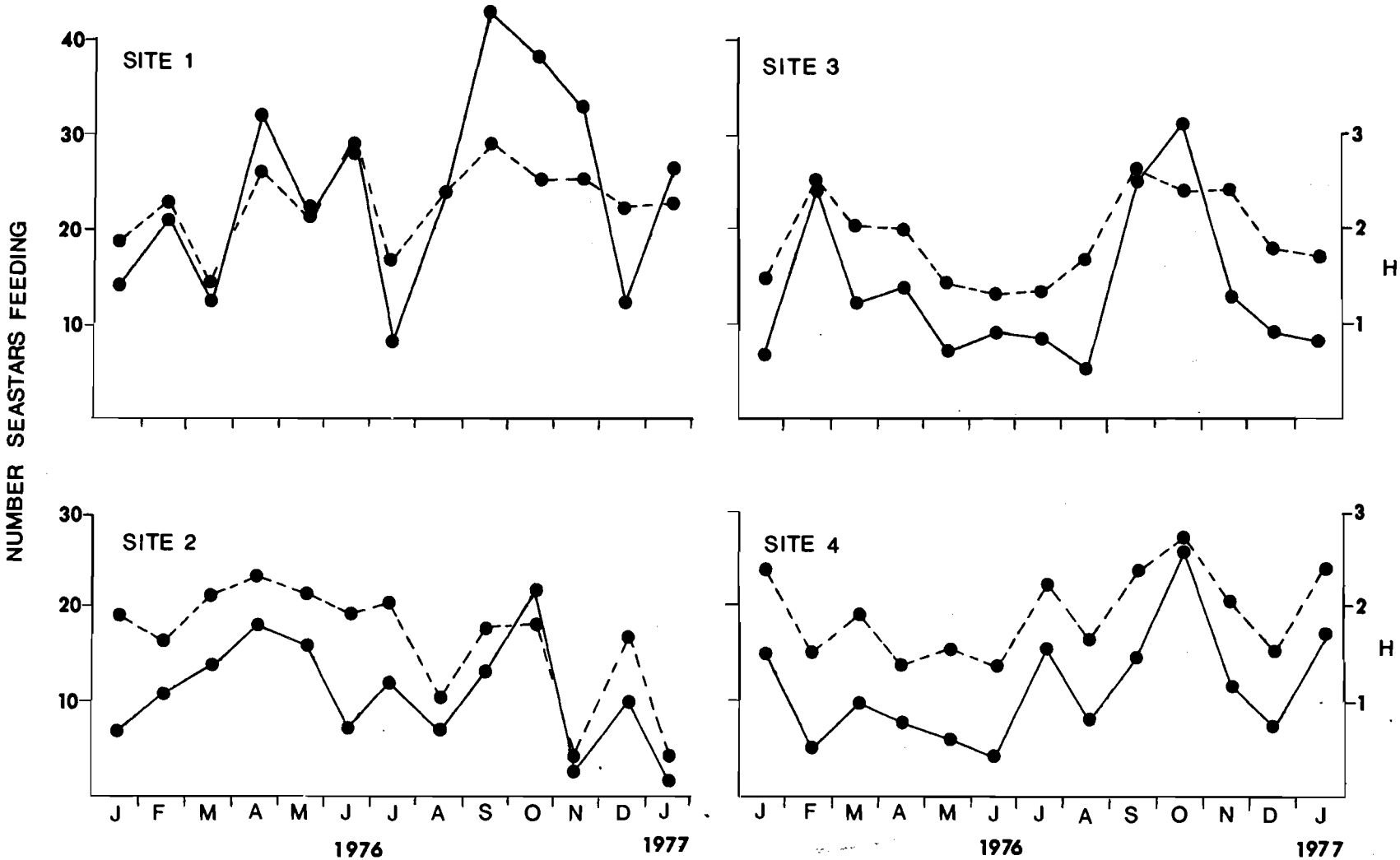

NUMBER SEASTARS FEEDING
SITE 1
SITE 2
SITE 3
SITE 4
40
30
20
10
3
2
1
H
J F M A M J J A S O N D J
1976
1977

TABLE 4.4. Monthly composition of the diet at Site 1.

	NUMBER EATEN												
	J	F	M	A	M	J	J	A	S	O	N	D	J
T. aurantium						1							
S. borealis	4	1	1	8									
I. maorianus		5		1	5	2	1	2	4	3	3	2	3
O. neglectus		1		2							1		
A. glaucus		1				1							
S. pelliserpentis				1		1			1	3		1	1
Chiton (indet.)		1											
H. iris				1		1		1	2				
C. radians									1		1		
C. ornata						1							
C. denticulata												2	
P. corticata		1						1					
Eatoniella sp.				6		2		1	6	3	1		
Estea sp.			2						2				1
R. chathamensis		1			1						1		
Zeacumantus sp.				2		1		2		1	1		
R. varia				2			2	1			2		
M. aethiops	2	3	3	1	4			1	2	3	3	3	2
M. dilatatus	1			3	1	1				1	2		1
C. tessellata									2	4	1		1
A. lugubris			1										
Trochids (indet.)									1	1			
T. smaragdus	1	2	5	3	3	6	2	4	8	7	3	2	5
C. maculosa		1	1			1						1	
C. glandiformis				1	1	1						1	
B. vitatum										1			1
B. bicinctum				1									
A. maoriana	2					2		1	2				1
M. edulis									1				
P. crassicosta	1				1	1						1	1
Z. disculus								1					
N. elegans										1			
O. maorum										1			
S. zelandica						2			2		1		
C. brunnea							4				3		
E. plicatus					2				2				
E. obtusum				3					1				2
Isopod (indet.)									1				
P. elongatus				1					1				
E. producta				1		2		1		1			
C. novaezelandiae								1	1		1		
P. chabrus											1		
P. novaezelandiae										3	1	1	1
N. ursus									2				
Notomithrax sp.				1									
E. chloroticus		1											
O. fasciata						1			1				
Trypterygion sp.						1							
Fish eggs (*Diplocrepis* sp.)								2	1				
Fish eggs (*Dellichthys*)											1		
Crustaceans (indet.)	1	1							1			1	
Everted stomach	2	4	4	2	5	5	2	5	6	11	9		7
Total species	8	13	5	18	11	18	6	14	23	15	18	10	14
No. feeding	14	21	12	32	21	29	8	24	43	38	33	12	26
Total observed	37	40	42	107	99	100	46	93	130	116	134	40	131

TABLE 4.5. Monthly composition of the diet at Site 2.

PREY	NUMBER EATEN												
	J	F	M	A	M	J	J	A	S	O	N	D	J
S. borealis		2		1			1						
I. maorianus		2	3	1		1			7	4		3	
O. neglectus	1			1	2				1	2			
A. glaucus		1		2	2							1	
E. nobilis	1												
A. zelandicus							1						
H. iris		1			1								
C. radians	2		1		1	1							
C. denticulata					1								
P. corticata	1												
S. breviculus	1												
Eatoniella sp.			4	2									
Estea sp.			1				1			1			
R. chathamensis			4										
M. aethiops		3		3	3	1	3	2					
M. dilatatus			1	4	4	2	1	7	2	15	2	3	2
C. tessellata					1		2	1	2			1	
T. smaragdus										1			
C. glandiformis					1	1							
A. maoriana	1												
P. crassicosta			2			1				1			
Squid (indet.)				1									
S. zelandica					1				1				
E. obtusum									2	3		2	
P. elongatus				1									
E. producta						1				2			
P. novaezelandiae				1								1	
N. ursus			2						1				
C. intestinalis										1			
Fish eggs (*Diplocrepis* sp.)								1					
Crustaceans (indet.)			1	1									
Everted stomach	1	4	3	3	1	1	4		1	4		3	1
Total species	7	6	10	12	11	7	8	4	8	10	2	6	2
No. feeding	7	11	14	18	16	7	12	7	13	22	2	10	2
Total observed	21	27	36	46	40	36	31	21	38	52	24	21	20

TABLE 4.6. Monthly composition of the diet at Site 3.

PREY	NUMBER EATEN												
	J	F	M	A	M	J	J	A	S	O	N	D	J
S. borealis		2		1									
I. maorianus	1	3		1			1	1	7	3	1		
O. neglectus		2	1				1		1	3	2		
A. glaucus											2	1	1
S. pelliserpentis												1	
Chiton (indet.)											1		
H. iris			1										
C. radians		1	1							2			
C. denticulata					1								
P. corticata		1	1										
Eatoniella sp.									2	3			
Estea sp.										1	1		
R. chathamensis									2	1			
Zeacumantus sp.		1							1				
R. varia		2		2		2	1	2	3	6			2
L. unifasciata									1				
M. aethiops	1	4	2	1		1				1	1		
M. dilatatus				4		4		2	2	8	2	3	
C. tessellata					1	2				4	1		
A. lugubris										1			
T. smaragdus		1					1					1	
C. glandiformis					1				1				
Cominella sp.			1										
B. vitatum	1												
A. maoriana									1				
M. edulis													1
H. australis			1										
P. crassicosta													1
S. zelandica						1			2				
C. brunnea										1			
E. obtusum		2	1	4				1	2	6		1	
D. varicolor											1		
Isopod (indet.)									1				
T. oculatum		3											
E. producta	1			1									
C. novaezelandiae					1								
P. chabrus				1									
P. novaezelandiae												1	
N. ursus											1		
O. fasciata													1
P. regularis								1					
C. intestinalis		1											
M. humboldti										2			
Fish carcass											1		
Everted stomach	3	5	4	2	3	1	4	1	3	1	2	3	2
Total species	5	13	9	9	5	6	5	6	14	15	12	7	6
No. feeding	7	24	12	14	7	9	8	5	25	31	13	9	8
Total observed	19	63	31	48	40	29	30	21	82	80	49	20	51

TABLE 4.7. Monthly composition of the diet at Site 4.

PREY	NUMBER EATEN												
	J	F	M	A	M	J	J	A	S	O	N	D	J
S. borealis	2												
I. maorianus						1	3			4		5	
O. neglectus	2	1			1		1		2	1	1		
A. glaucus	1	1	1		1	1	2	1	1	3	2		2
E. nobilis			1								1		
A. zelandicus									1				
G. obtecta													1
Chiton (indet.)							1						
H. iris			1								2		
H. australis										1			
C. radians	1			2	2					1	1	1	1
C. denticulata													2
P. corticata	2									2			1
Eatoniella sp.		2		7		1				1			1
Estea sp.		3								1		5	
R. chathamensis													2
R. varia			3					5	4	1			2
M. aethiops				1	1			1		2	1	1	1
M. dilatatus	1		2			1	3		1	2	2		
C. tessellata							1		1	1			
T. smaragdus			2										
C. glandiformis									3				
B. bicinctum													1
A. maoriana	1						1		2	1			
M. zelanicus									1				
S. zelandica							1			3	3		1
M. spinosa	1												
E. obtusum							2		1	1			
C. novaezelandiae											1		
P. chabrus			1					1		1			
H. rotundifrons			1				1						
P. novaezelandiae									1			1	
N. ursus				1									
N. minor							1						
Notomithrax sp.				1					1				
P. regularis													1
D. morelandi										1			
Fish eggs (*Diplocrepis* sp.)	1							1					
Fish carcass	1							1					
Nudibranch (indet.)									1				
Everted stomach	3	2	2	1	1		5	1	1	3		2	3
Total species	11	5	8	6	5	4	12	7	13	19	9	6	13
No. feeding	15	5	10	8	6	4	16	8	15	26	12	7	17
Total observed	25	19	26	23	25	26	73	24	65	74	34	26	70

localities may infer that dietary composition is temporally dependent. Obviously, in the present case, this is not so and data which suggest this are merely the result of the non-continuous sampling procedure.

Trochids, chitons, turbinids and decapods appeared in the total diet (i.e. four sites combined) every month, but at the specific level, only four (*I. maorianus*, *A. glaucus*, *M. aethiops* and *T. smaragdus*) were eaten every month. At site 1, only *T. smaragdus* was eaten every month, whilst *I. maorianus* and *M. aethiops* occurred in all but one monthly sample. At site 2, no one species was recorded as prey every month, but *M. dilatatus* appeared in 10 of the sampling months, *I. maorianus* in 7, and *M. aethiops* in 6. *I. maorianus* and *R. varia* occurred in 8 of 13 monthly samples at site 3, *M. aethiops*, *M. dilatatus* and *E. obtusum* appeared in 7. At site 4, *I. maorianus* appeared in only 4 of 13 samples, whereas *O. neglectus*, *M. aethiops*, *M. dilatatus* and *Cellana radians* were present in 7 monthly samples (Tables 4.4 - 4.7).

The impact of predation on the prey community.

The impact of *A. scabra* on its prey community can be assessed by comparing the number of prey consumed by the predator with the number of spatially co-occurring prey. The latter parameter can be measured directly, but the former must be estimated. Two methods have been proposed for the estimation of prey removal rates in asteroids. Paine (1969b) proposed the formula: No. prey eaten/yr. = A x B x C x D. (where A = monthly proportion feeding, B = daily feedings, C = days in month, D = mean no. prey eaten by feeders). These monthly values are then summed to provide the annual rate. A second formula suggested by Menge (1972a) was: No. prey consumed/m^2/yr. = $\frac{A \times B \times C}{D} \times E \times F$. (where A = mean proportion feeding, B = dietary proportion of the prey, C = available foraging hrs./day, D = consumption time for average prey, E = seastar density, F = days/yr. spent foraging.) Both formulae

account for the fact that all seastars do not feed at every opportunity, but Paine's method takes no account of actual predator density and, therefore Menge's formula was used to provide the values given in Table 4.8. For *A. scabra* the following assumptions were made. The number of foraging hours per day (C) was 12, the consumption time for average prey (D) was 6h, and the number of days per year spent foraging (F) was 200. The first was selected as the general period of immersion for this species, and the second was selected for two reasons. Firstly, if average consumption time is less than 6h, the validity of the estimate is not challenged as foraging does not recommence until the following high tide period. Secondly, laboratory observations indicated that all prey, with the possible exception of *T. smaragdus*, are consumed within 6h of capture. Days/yr. spent foraging is estimated from the number of hours the water level is above +0.3m (N.Z. Tide Tables, Marine Division, Ministry of Transport, Wellington).

With some notable exceptions, the number of prey consumed/m^2/yr. was similar for all prey species at all sites (Table 4.8). Thus, *T. smaragdus* (at site 1) and *M. dilatatus* (at site 2) were removed at rates one order of magnitude greater than those at other localities. At each site, the proportion of each prey removed corresponded closely with its dietary proportion. The totals of the nine major prey species consumed/m^2/yr. at each site were similar also, despite the different proportional basis of site diets. The relatively elevated value of the total removal rate at site 2, was due entirely to heavy predation pressure on *M. dilatatus* at this location.

When removal rates are compared with mean prey densities, a measure of percentage removal of spatially co-occurring prey/m^2/year can be gained (Table 4.9). Prey densities were measured at different times of the year, and thus should take into account temporal variability in prey numbers.

TABLE 4.8. The number of prey consumed/m^2/yr.

PREY SPECIES	SITE 1	2	3	4
I. maorianus	0.65	1.15	0.64	0.5
O. neglectus	0.08	0.38	0.35	0.35
A. glaucus	0.04	0.33	0.13	0.62
Eatoniella sp.	0.4	0.33	0.18	0.47
R. varia	0.14	0	0.71	0.58
M. aethiops	0.57	0.82	0.39	0.31
M. dilatatus	0.2	2.18	0.89	0.47
T. smaragdus	1.08	0.05	0.1	0.07
E. obtusum	0.12	0.38	0.6	0.16
Total	3.28	5.62	3.99	3.53

TABLE 4.9. Mean, range, and standard deviation of prey density and percentage removal rates.

PREY	RANGE (No./m^2)	MEAN DENSITY (No./m^2)	S.D.	NO. QUADRATS ($0.25m^2$)	% REMOVAL
I. maorianus	0-240	14.3	18.03	33	5.1
O. neglectus	0-20	1.0	1.33	33	29.0
A. glaucus	0-20	1.29	1.73	33	21.7
R. varia	0-28	1.4	2.12	26	34.0
M. aethiops	0-124	4.66	6.98	33	11.2
M. dilatatus	0-32	2.8	2.9	19	33.3
T. smaraguds	0-74	8.8	4.94	19	3.6

The high proportion of *M. dilatatus* removed was again due to its importance as prey at site 2. Only 11.2% of another trochid, *M. aethiops*, was eaten. Although *I. maorianus* was the most important dietary chiton, only 5.1% of these animals were removed as compared with more than 20% of both *A. glaucus* and *O. neglectus*. A small proportion of *T. smaragdus* was eaten, in spite of its role as the chief food source of *A. scabra* at site 1. In contrast, 34% of the littorinid *R. varia* were removed during the year. Evidently, the proportion of a single prey species removed is independent of its density.

CHAPTER 5. SELECTIVE FEEDING

INTRODUCTION

A wealth of subjective assessments of "selectivity" in asteroid feeding has appeared since Galtsoff and Loosanoff (1939) reported that *Asterias forbesi* preferred soft-shelled clams to other food. Ferguson (1969) stated that "although many echinoderms are able to subsist on a wide variety of foods, they may still exhibit marked preferences when provided with a selection". Only four truly quantitative studies have been conducted on prey-discriminant feeding in asteroids (Landenberger, 1968; Christensen, 1970; Birkeland, 1974, Menge and Menge, 1974). Landenberger (1968) concluded, as a general principal, that prey preferences existed, were the rule rather than the exception, and could be ranked in a hierarchy. Christensen (1970) suggested that most members of the genus *Astropecten* possessed the ability to discriminate between prey species. This view was not supported by Wells *et al.* (1961) who discovered 91 species of invertebrates, representing 5 phyla, in the stomachs of 124 *Astropecten articulatus*. Their latter findings, however, were contrary to those of Hulings and Hemlay (1963) who noted that *A. articulatus* preferred small gastropods to crustaceans and bivalves. Further, Massé (1966) regarded *A. johnstoni* as an indiscriminate feeder. Recent work by Ribi *et al.* (1977) and Ribi and Jost (1978) has shown that *A. aranciacus* and *A. bispinosus* consumed bivalves, gastropods and echinoids at a level disproportionate to their occurrence in the prey community. Clearly, the degree to which asteroids select prey remains the source of some controversy.

In those seastars that do select prey, the ability to discriminate between prey organisms may be refined to the point that

only single species are eaten (Mauzey *et al.*, 1968; Birkeland, 1974; Dayton *et al.*, 1974), or to the extent that higher taxonomic groups are preferentially consumed. Examples of the latter include *Luidia sarsi* which preys exclusively on ophiuroids (Fenchel, 1965), *L. ciliaris* on echinoderms in general (Brun, 1972), *Asterias rubens* on mussels (Hancock, 1955), and *A. vulgaris* on oysters (Whittle and Blumer, 1970). The crown-of-thorns starfish, *Acanthaster planci*, has a distinct preference for certain types of coral (Collins, 1975), and Ormond *et al.* (1976) speculated that this species was able to form an olfactory search image for its favoured prey.

Specialisation on a particular food may alter along the geographical range of a species. For example, *Dermasterias imbricata* is a food specialist on the sea pen *Ptilosarcus gurneyi* where the latter occurs in beds in Puget Sound (Birkeland, 1974), but is a scavenger of bottom detritus and moribund animals in southern California (Hopkins and Crozier, 1966). Food preferences may change also according to the age, size and physiological state of the predator (Ferguson, 1969), or may vary seasonally (Menge, 1972b).

The objectives of this study were to determine if *Astrostole scabra* was able to discriminate between prey types, and at what taxonomic level. Further, if discrimination was demonstrated, to discover whether common prey species could be ranked in an order of preference.

MATERIALS AND METHODS

The animals used in this study were collected from the sites described in detail in Chapter 4. Prey organisms were collected immediately before the commencement of experiments, but seastars were maintained, without food, in open-circulation seawater aquaria at 9.4 - 10.8^{o}C for 27-30 days prior to use. This starvation period

ensured that all experimental seastars had not fed for at least 4 weeks, and could be regarded as being at comparable levels of hunger at the start of each experiment. This treatment overcame also the problem of ingestive conditioning i.e., "a predator prefers a certain prey species after it has fed on it for some time" (Landenberger, 1968; Christensen, 1970; Collins, 1975; Ormond *et al.*, 1976). Learning ability in asteroids is short-term (Landenberger, 1966; Valentincic, 1978) and should have had no influence on results. All experimental seastars were immature with R = 60.1 - 174.3mm. Seasonal variations in food preferences were eliminated by carrying out the experiments between 21 July and 21 September 1977 (winter).

To determine prey preferences, individuals of *A. scabra* were presented with a choice of prey in separate 500 x 400 x 90mm plastic trays. Each tray was roofed with a 2mm meshwork plastic frame to prevent escape of seastars or prey, and was supplied continuously with fresh seawater. The effects of container geometry on prey choice were therefore identical in every case. The confinement of animals within small containers was assumed to negate the effects of prey escape reactions (Chapter 6). Each experiment started at 2300h and was terminated at 0900h. At the end of this interval, seastars were removed, and digested prey were identified and counted. Seastars were held for a further 27-30 days without food, before being used in subsequent experiments. Two series of prey choice experiments were carried out, both utilising organisms known to be important, numerically, in the natural diet (Chapter 4). The first choice set (Experiment 1) consisted of three individuals each of *Amaurochiton glaucus*, *Ischnochiton maorianus* and *Melagraphia aethiops*. The second choice set (Experiment 2) comprised three individuals each of *Amaurochiton glaucus*, *Onithochiton neglectus* and *Micrelenchus dilatatus*. This latter choice set was established after the results of experiment 1 were known, and

included the least preferred species in that set. Experiment 1 was repeated seventy times, with no prey being consumed in twenty-eight runs. Experiment 2 was repeated sixty-four times, and no results were obtained in twenty-three instances. The dimensions of prey offered are given in Table 5.1. Sizes are expressed as anterior-posterior length for chitons, and shell height for trochids.

These sized animals typify those available to seastars in nature (Chapter 7). Prey were arranged randomly in trays before the introduction of seastars.

RESULTS

In both experiments, *A. scabra* discriminated between the different prey species offered, and consumed one species significantly more often than others (Table 5.3). The rank order of prey preferences from experiment 1 was *I. maorianus*> *M. aethiops*> *A. glaucus*. *I. maorianus* was eaten significantly more often than *M. aethiops* ($x^2 = 22.3$, $p < 0.001$), which was eaten according to the abundance provided, and *A. glaucus* was discriminated against ($x^2 = 9.1$, $p < 0.025$).

In experiment 2, the established rank order of prey preferences was *A. glaucus*> *O. neglectus*> *M. dilatatus*. In this experiment, *A. glaucus* was strongly favoured ($x^2 = 23.3$, $p < 0.001$), *O. neglectus* was consumed at a level proportionate to the abundance provided, and *M. dilatatus* was discriminated against ($x^2 = 29.0$, $p < 0.001$) to the extent that not one of the 192 individuals offered during the experiment was eaten (Table 5.3). As *A. glaucus* was the least preferred species in choice set 1, and was the favoured species in choice set 2, the rank order of prey preferences for the five species used was:- *I. maorianus*> *M. aethiops*> *A. glaucus*> *O. neglectus*> *M. dilatatus*.

The results from experiment 1 reflect very well the observed

TABLE 5.1. Range of prey sizes offered in selective feeding experiments.

SPECIES	SIZE RANGE (mm)
I. maorianus (chiton)	9.4 - 39.6
A. glaucus (chiton)	11.5 - 38.7
O. neglectus (chiton)	10.7 - 34.8
M. aethiops (trochid)	3.1 - 16.5
M. dilatatus (trochid)	2.4 - 7.3

TABLE 5.2. Percentage inclusion of species in the natural diet (from Chapter 4).

SITE	*I. maorianus*	*M. aethiops*	*A. glaucus*	*O. neglectus*	*M. dilatatus*
1	8.86	7.58	0.56	1.12	2.8
2	11.6	8.28	3.31	3.86	22.6
3	8.73	5.33	1.94	4.85	12.1
4	6.73	4.14	8.29	4.66	6.21

frequency of *I. maorianus*, *M. aethiops* and *A. glaucus* in the whole natural diet (8.86, 6.51 and 2.99% respectively) (Chapter 4). The results of experiment 2, however, are not in accord with field observations. At Kaikoura, *M. dilatatus* was the numerically dominant prey species, but these experiments have shown it to be strongly discriminated against when alternative prey were present. Indeed, the rank order of preference, viz - *A. glaucus*> *O. neglectus*> *M. dilatatus* was the reverse of the numerical importance of these species in the diet of wild populations. This was not true of study site 4, where the order was *A. glaucus*> *M. dilatatus*> *O. neglectus* (Table 5.2) which corresponded, in part, with the preferences isolated in the laboratory.

Observations made at study site 4 also differ markedly from results gained in experiment 1, in that *A. glaucus* occurred as a food item there, more commonly than either *M. aethiops* or *I. maorianus*, yet was discriminated against in the feeding experiment.

Although strong preferences for particular prey existed at the specific level, no clear distinction was evident at the familial level i.e. chitons and trochids appeared to be more-or-less equally attractive as food. It was noted during the course of these experiments, that the consumption of a particular prey item did not preclude the subsequent or simultaneous capture of another prey item of the same or a different species (Table 5.3). In both experiments, the favoured prey species represented about 63% of all items eaten.

TABLE 5.3. Results of prey choice experiments 1 and 2.
(+ = 1 item eaten).

	PREY EATEN EXPERIMENT 1			PREY EATEN EXPERIMENT 2		
	I. maorianus	*A. glaucus*	*M. aethiops*	*A. glaucus*	*O. neglectus*	*M. dilatatus*
	+++			+		
	++			+		
	+++			+		
	++			+		
	+++			++		
	++			++	+	
	+++			+		
			+	+		
	+++		+	+	+	
		+		++		
	+		+	++		
	++		++		+	
		+	+		+	
	+			++		
	+		+	++		
	++	+	+	++		
		+		+	++	
	+++		+	+	+	
	+	+	+	+		
			+		++	
	+	+			+	
	+		+	+++	+	
		++		++		
	+			+	+	
			+	+		
	+				+	
	+				++	
	++			++	+	
			+	+		
	++			++	+	
	+			++	+	
		+		++	++	
	+			+++	+	
			++	+		
	++			++	++	
	+	+		+	+	
	+			+++	++	
	+			++		
	+		++	+	+++	
	+++	+		+	+	
	+		+	+	++	
		+				
TOTAL EATEN	53	12	19	55	32	0
% OF PREY EATEN	63.0	14.2	22.6	63.2	36.7	0
TOTAL PREY OFFERED	210	210	210	192	192	192

CHAPTER 6. PREY ESCAPE REACTIONS

INTRODUCTION

Some organisms react strongly to contact with predatory asteroids. The general response is swift movement away from the source of stimulus, and this has been well documented since early Maoris induced the flight response in abalone, with hand-held seastars, as a simple means of breaking the mollusc's grip on the substrate (Feder, 1972). Most research has been directed toward the nature of responses in molluscs; the first description of a response was for *Nassarius millepunctata* to contact with the asteroid *Marthasterias glacialis* (Schiemenz, 1896). Molluscs may show an escape reaction only to specific asteroid species (Fänge, 1963; Edwards, 1969), to all members of a genus (Yarnall, 1964), to members of an order (Margolin, 1964b), or to higher taxa (Margolin, 1964a; Thomas and Gruffydd, 1971; Margolin, 1975; Phillips, 1976). For example, the anemones, *Stomphia coccinea* and *Actinostola* sp. respond to both predatory asteroids and the nudibranch *Aeolidia papillosa* (Mauzey *et al.*, 1968). In some cases specificity is correlated with known predator-prey relationships, however, some organisms will react to asteroids they do not encounter normally in nature (Crump, 1968). In an interesting reversal of the "normal" situation, the echinoid *Diadema antillarum* has an escape response from the mollusc *Cassis tuberosa* (Snyder and Snyder, 1970).

The numerous investigations into avoidance and escape reactions in molluscs have created little controversy, however, Feder (1959, 1963, 1967, 1972) and Cox (1962) considered that abalone were preyed upon by seastars only when moribund or dead. Montgomery (1967) termed the reactions of *Haliotis assimilis* and *H. rufescens* to the close proximity

of seastars, "flight responses", rather than escape responses; he shared Feder's view that no predator-prey relationship existed between seastars and healthy abalone. Montgomery considered further, that it was "hardly feasible" that the responses of abalone in nature were effective. In contrast, Bonnott (1930), MacGintie and MacGintie (1949), Forster (1962) and Shepherd (1975) recorded predator-prey relationships between abalone and seastars, and Livingstone (1952) reported that areas rich in seastars yielded few abalone. Abalone appear in the diet of *A. scabra* at Kaikoura and Tasmania, where the asteroid is called "the purple abalone eater" (Chapter 4; Dartnall, 1969a, pers. comm.). D.C. Wolfe (pers. comm.) noted that abalone frequently were pursued and occasionally captured in waters around Maria Island, Tasmania. B. Tunbridge (unpublished field notes) has observed *Haliotis iris* being caught and digested by *A. scabra* near Wellington. During the course of my study, both *H. iris* and *H. australis* were frequently seen fleeing from foraging *A. scabra*. The key to the disagreement on abalone-seastar relationships may be due to factors identical with those found in the interaction between several species of predatory asteroids, the holothurian *Parastichopus californicus*, and scallops *Chlamys* spp. in Puget Sound - "the very success of a response may lead to an apparent lack of correlation - the response may effectively remove the prey from the predator's diet" (Mauzey *et al.*, 1968).

It is known that particular compounds emanating from seastars are responsible for initiating reactions in molluscs. Ward (1965a, 1965b) designated these "stimulatory carbohydrates" of an amino-polysaccharide nature, but Mackie (1970) and Turner *et al.* (1971) have shown them to be surface-active steroid glycosides (steroidal saponins). These chemicals act in free equilibrium with a protein complex (Mackie *et al.*, 1968) on chemoreceptors in the molluscan head, foot, cephalic tentacles and mantle margin (Phillips, 1975b). Steroid glycosides may

damage these chemoreceptors (Mackie, 1970), thus the ultimate fatigue or habituation of molluscs and their subsequent failure to respond to the constant presence of, or repeated stimulation by predatory asteroids, in aquaria, is well documented (Bullock, 1953; Feder, 1963; Margolin, 1964a). In dry, extracted form, steroid glycosides are stable in light, air and heat (60°C) (Feder and Lasker, 1964). Depending on species, these substances are concentrated in the tube foot epidermis (Feder and Lasker, 1964), the furrow epithelium and marginal spines (Mayo and Mackie, 1976), or both the oral and aboral surfaces of seastars (Feder and Arvidsson, 1967), and are continually lost to the surrounding medium (Feder and Arvidsson, 1967). This causes sensitive organisms to respond at a distance (Feder and Christensen, 1966; Phillips, 1975a, 1977), or upon contact (Feder, 1959; Fänge, 1963; Margolin, 1975; Fager, 1968; Edwards, 1969; Stephens and Boyle, 1978). The former are designated avoidance reactions and the latter escape responses.

Several authorities have suggested that all forcipulate asteroids produce avoidance-inducing compounds. Doering (1976) proposed that seastars induce movement in potential prey to minimize the chances of mistakenly attacking a dead organism, and to maximize the potential cues for prey recognition. This standpoint cannot be justified on a number of grounds. Firstly, many seastars do eat carrion; secondly, the preferred food of some asteroids is sessile (Landenberger, 1968) or non-responsive (Chapter 5); thirdly, seastars can detect food by chemosensory means alone (Smith, 1940; Needler, 1941; Christensen, 1970; Whittle and Blumer, 1970; Castilla, 1972; Zafiriou, 1972; Zafiriou *et al.*, 1972; Valentincic, 1973); fourthly, movement alone will not distinguish potential prey from water-borne debris and waving seaweed; and finally, effective avoidance responses might render actual contact rare (Phillips, 1976).

Non-asteroid echinoderms can detect the close presence of, or contact with, predatory asteroids and have various responses to them. Some echinoids have a pedicellariae response (Jensen, 1966; Dix, 1969; Rosenthal and Chess, 1972), in which the spines are flattened against the test to allow the pedicellariae to pinch the seastar's tube feet. Others have a running response (Snyder and Snyder, 1970). A combination of both is also recorded (Dayton *et al.*, 1977). Vasserot (1964) suggested that the echinoid *Arbacia lixula* used a combination of chemical defence and spine erection to deter *Marthasterias glacialis*. The holothurian *Parastichopus californicus* displays a swimming response from predatory seastars (Mauzey *et al.*, 1968; Feder, 1972), and the ophiuroid *Ophiocomina nigra* has an escape response from *Luidia ciliaris* (Brun, 1972).

In addition, some seastars are able to detect their own predators either at a distance (Castilla and Crisp, 1970; Mayo and Mackie, 1976), or by contact (Feder, 1967; Mauzey *et al.*, 1968; Birkeland, 1974; Dayton *et al.*, 1977). The normal response is movement away, and frequently a ray is autotomised in the process. This is a most intriguing situation, as the bulk of asteroid predators are themselves asteroids. It is difficult to reconcile the possibility that fleeing seastars respond to the non-species specific (Mauzey *et al.*, 1968) steroidal exudates of a potential predator, but not to their own exudates, and the recognition of a nearby potential predator probably involves another cue. Dayton *et al.* (1977) reported several instances of distance response of prey to the presence of foraging *Meyenaster gelatinosus* at a speed and distance too great to be readily explained by chemical diffusion, but they found a lack of response to quiescent seastars. Although the echinoids *Diadema antillarum* and *Strongylocentrotus* spp. react to the nearby injury or predation of congeners by fleeing, presumably in response to chemical diffusion (Snyder and Snyder, 1970; Mauzey *et al.*, 1968), *Loxechinus*

albus behaves in an opposite manner. This led Dayton *et al.* (1977) to suggest that "squeaking" of ossicles in foraging asteroids may be the extra cue, and that potential prey could therefore discriminate between foraging and non-foraging seastars.

The actual effectiveness of escape reactions often depends on the size of the reacting organism (Fager, 1968; Christensen, 1970; Phillips, 1977), and Feder (1967) concluded - "in most cases responses are significant only when the seastar is small relative to the reacting organism, which can therefore readily move away". In nature, escape reactions have been deemed to have been successful if the responding species is not eaten according to its abundance in the potential prey community (Feder, 1963; Martin, 1970; Phillips, 1976; Dayton *et al.*, 1977). However this approach assumes that abundance is the only critical factor in the determination of prey removal rates. Clearly, this is not so. For example, habitat structure may influence the success of escape reactions as a vertical rock face may allow a more effective expression of a response than a slope (Phillips, 1976). *Tegula funebralis* has an escape response from *Pisaster ochraceus* (Yarnall, 1964), but Paine (1969b) found that 25-28% of adult snails were still consumed within interspecific overlap areas in boulder habitats at Mukkaw Bay. In addition, physical factors can affect response efficiency. Dickie and Medcof (1963) showed that sudden, small temperature changes caused debility in *Placopecten magellanicus* and that this hampered escape and allowed capture by *Asterias vulgaris*.

Most studies of escape and avoidance behaviour are confined to Northern Hemisphere animals. Published observations on New Zealand animals include those of Bennett (1927) on *Haliotis iris* and *H. australis*, Clark (1958) on *Melagraphia aethiops*, and Crump (1968) on *Struthiolaria papulosa gigas*, and in this study, 21 species of invertebrates known to occur in the diet of *A. scabra* at Kaikoura, and

two non-dietary species were tested for their reaction to contact with the seastar.

MATERIALS AND METHODS

Animals tested for the presence of escape reactions were collected from beneath intertidal rocks 1-3h prior to the commencement of experiments. They were first allowed to settle in aquaria supplied continuously with fresh seawater. Stimulatory seastars were either collected at the same time or were part of a stock population maintained in the laboratory. Prey specimens were stimulated by contact with either a hand-held seastar, or by the seastar itself as it wandered around the aquarium. In some cases, a single tube foot torn from a seastar and held in forceps was used as a contact stimulator. Between each experiment, aquaria were emptied and scrubbed to eliminate the effects of any chemical residues. All experiments were conducted in natural light and at ambient seawater temperature (9.8 - 10.4^{o}C).

Wherever possible, results obtained in the laboratory were compared with responses of animals in nature when stimulated with an intact, hand-held seastar. This procedure was undertaken to overcome the potential effects of trauma caused by the removal of an organism from its normal environment. Field experiments were made only in tidepools from which seastars were absent, and in which all potentially responsive animals were immobile. An escape reaction was recognised as atypical, exaggerated, or accelerated movement by the prey.

RESULTS

Of 21 dietary species, 14 exhibited reactions to contact with

A. scabra. All but one of these, the echinoid *Evechinus chloroticus*, were molluscs. A further two non-dietary molluscs, *Haliotis virginea* and *Diloma arida*, showed escape reactions.

Chitons

Amaurochiton glaucus and *Onithochiton neglectus*

Escape reactions in both species were identical. The preliminary response consisted of an immediate retreat backwards, forwards or sideways at 180° to the point of stimulation. With repeated or prolonged stimulation, the girdle was raised in an irregular fashion, and the chiton ascended an inclined surface, when present, and left the water. Seastar surface water dripped from above caused test specimens to return to water. Both species could be guided around an aquarium with a single tube foot as stimulator. The rate of locomotion during escape reactions was insufficiently rapid for these species to outrun a pursuing seastar. In nature, *A. glaucus* was seen to share the underside of rocks with quiescent seastars.

Abalone

Haliotis iris and *H. australis*

The dramatic escape responses of these two species were described by Bennett (1927). He wrongly identified his stimulatory seastar as *Coscinasterias calamaria* which does not occur at Kaikoura; his description of the seastar does correspond with that of *A. scabra*. The responses to contact in both these species comprised four phases, and in essence paralleled those described by Montgomery (1967) for *H. assimilis* and *H. rufescens* to contact with *Pycnopodia helianthoides* and *Pisaster ochraceous* and by Feder (1963) for *H. rufescens* and *H. cracherodii* to contact with *P. ochraceous*. Immediately after contact, the epipodium was protruded from beneath the shell, and inflated. Epipodial tentacles were then extended and probed the

surrounding water. The second response phase was the raising and violent whirling of the shell through an arc of up to 180°. This latter motion often broke the hold of the asteroid's tube feet. Response phase three included both a continuation of shell whirling and locomotion away from the seastar at rapid speed. When moving at speed, the molluscs easily outran seastars. The final response phase was the emission of mucus, and in mature specimens, sperm or ova through respiratory pores in the upper shell surface. Stimulated abalone frequently left the aquarium and dropped to the laboratory floor. On a number of occasions, *H. iris* ultimately failed to respond to the constant presence of seastars in aquaria. At Kaikoura, *H. iris* and *H. australis* were seen fleeing from foraging *A. scabra* in the field. In addition, at low tide periods, both species could be found occupying the underside of a single rock, with *A. scabra*, without the former two species showing any signs of escape behaviour. Three factors indicate that both *H. iris* and *H. australis* are able to discriminate between foraging and non-foraging *A. scabra*. Firstly, if the co-habited rock is inverted, both abalone species retreat rapidly to the submerged side. This indicates that their receptor systems are not inoperative (Fig. 6.1). This may be a geotactic response. Secondly, the normally turbulent water movement in the intertidal sites surveyed would have prevented a localised build-up of steroid glycosides, and the consequent habituation or fatigue of appropriate chemoreceptors. Thus, the abalone should still respond to the presence of the seastar. Finally, and most importantly, *H. iris* and *H. australis* were seen to tolerate only the presence of quiescent seastars, mobile seastars consistently elicited the escape response.

FIGURE 6.1: Upper left. Two *H. iris* in close proximity to a quiescent *A. scabra* on the exposed side of an inverted rock.

Upper right. One *H. iris* and one *H. australis* in the same situation. The epipodium of the *H. australis* has been protruded from beneath the shell, epipodial tentacles are clearly visible, and the animal has begun to move.

Lower left. The *H. australis* has moved through an arc of approximately 90^{o} and climbed partially on to the shell of the *H. iris*.

Lower right. The *H. australis* has now moved through an arc of 180^{o} and is moving rapidly toward water. Shortly after this point, the animal had reached the underside of the rock.

Total elapsed time 30s. All photographs taken at site 4.

Limpets

Cellana radians, *C. ornata* and *C. denticulata*

Light, lateral stimulation of the limpet, *C. radians*, by an intact seastar produced jerky movements, slight "mushrooming" (in which the foot is extended vertically by elongation of the columellar muscle, to raise the shell above the substratum), and extension of the lateral tentacles and the middle fold of the mantle. With sustained stimulation, "mushrooming" was pronounced greatly, and the middle fold of the mantle was reflexed dorsally to cover the shell almost entirely. During contact periods, lateral mantle tentacles were waved constantly. Prolonged stimulation (i.e. for more than 30s) resulted in a reduction of "mushrooming" and movement away from the seastar at comparatively rapid speed. Some specimens left the aquarium at this point. These reactions are similar to the mantle response of *Diadora aspera*, the running responses of *Acmaea* spp. (Margolin, 1964a; 1964b), and the "mushrooming" of *Patella vulgata* (Feder, 1967). Tube feet which touched exposed mantle tissue were withdrawn rapidly, and the whole arm of the seastar was removed from the area of contact. *A. scabra* showed a general reluctance to consume limpets in the laboratory. This behaviour pattern resembled results gained by Margolin (1964a) when seastars touched the mantle tissue of *D. aspera*.

Responses elicited in *C. ornata* and *C. denticulata* were much less vigorous, and were identical except that no running response was observed. Crump (1969) was unable to detect any response by *C. ornata* or *C. denticulata* to contact with the forcipulate *Coscinasterias calamaria*.

Fissurellid gastropods

Scutus breviculus

The fissurellid, *S. breviculus*, exudes copious quantities of

mucus when handled. Few juveniles were found in the intertidal zone. Adults were insensitive to contact with *A. scabra*, perhaps because asteroid tube feet cannot adhere to mucus-coated tissue. It was concluded initially that an escape response was not present in this species (Clark, 1958). Early in 1977, I saw a single, large *S. breviculus* moving rapidly in an intertidal pool during low tide, a time when the species is normally inactive. A search in surrounding algae yielded a large *A. scabra*, apparently in pursuit of the mollusc. A short time later, I collected a small *S. breviculus* and tested the species' response to contact with *A. scabra* in the laboratory. The defensive response in *S. breviculus* consisted of expansion and raising of the mantle, turning away at 90° to the seastar, and rapid locomotion. The vigour of the response decreased with repeated stimulation. Only once was *S. breviculus* recorded as a prey item (Chapter 4), and large lesions on this specimen clearly indicated that it was moribund or dead prior to consumption.

Littorinid gastropods

Risellopsis varia

This small species has two types of defensive response. Individuals attached to inclined surfaces at the time of contact with a seastar merely released their grip on the substratum. Not only does this reaction immediately remove the endangered mollusc from the vicinity of the seastar, but in nature, wave action may wash it further away. When on a horizontal surface, *R. varia* lifted its shell clear of the substratum, and rotated it through 180°, many times, before moving, at varying angles, away from the seastar.

Trochid gastropods

Micrelenchus dilatatus

On contact with *A. scabra*, some specimens raised their shell clear of the substratum, and quickly rotated them through 180° several times; others showed no shell rotation. Following shell rotation, animals moved away in a direction opposite to the point of stimulus. If *M. dilatatus* was contacted at the anterior end while moving, it rotated through 180° and moved away. If stimulated from behind, the test specimens maintained their course but increased the rate of progression. If caught by a seastar, *M. dilatatus* retreated into its shell, and closed the aperture with its operculum.

Cantharidella tessellata

Escape responses in this species were broadly similar to those of *M. dilatatus*, except that shell whirling was not observed. Upon contact, *C. tessellata* became highly agitated, and moved away from the point of contact.

Melagraphia aethiops

The reaction of *M. aethiops* to contact with *A. scabra* was described by Clark (1958). With brief contact between the two, *M. aethiops* alters its direction of locomotion by 90°, and moves away at two to three times normal crawling speed. Inclined surfaces, when present, may be ascended for considerable distances and the trochid may come to rest well above the air/water interface. Some specimens could be induced to move higher still, by allowing seastar "drippings" to fall on them. With contact of more than 15s duration, the trochid lifted its shell clear of the substratum, and swung it violently, several times, through an arc of 180°. If overwhelmed, the trochid ceased moving, and sealed the shell aperture with the operculum. If digestion did not follow capture, the trochid moved away rapidly

immediately after its release.

The reactions of the three trochids described above, although differing in detail, were essentially alike and were very similar to the locomotory responses of many other trochids to stimulation by seastars. This supports Ansell's (1969) statement that, "the responses.....must be regarded as expressions of a behaviour pattern of great antiquity in the stock which gave rise to the group".

Whelks

Cominella maculosa

This species has no locomotory adaptation to contact with *A. scabra* and was never eaten in aquaria. After prolonged stimulation in the laboratory, the water closely adjacent to the mollusc became discoloured with a green discharge, which may have a defensive role, and could possibly anaesthetise the olfactory or tactile senses of the predator. A number of marine molluscan herbivores secrete compounds of an apparently distasteful nature when stimulated by a variety of potential predators (see review in Ansell, 1969).

Echinoderms

Evechinus chloroticus

Dix (1969) briefly mentioned the escape reaction of *E. chloroticus* to *A. scabra*. This response consisted of two, and possibly three aspects. First, *E. chloroticus* showed a running response from the seastar, and maintained a distance between itself and *A. scabra* in laboratory tanks. This behaviour is identical with that described for a number of other echinoids (Jensen, 1966; Snyder and Snyder, 1970; Rosenthal and Chess, 1972; Dayton *et al.*, 1977). Secondly, when cornered, the urchin used a pedicellariae response in which the spines are flattened against the test, allowing the globiferous pedicellariae

to close on the seastar's tube feet. This response has been noted in *Psammechinus miliaris* by Jensen (1966) and in *Strongylocentrotus purpuratus* by Rosenthal and Chess (1972). The success of this reaction was variable. Specimens of *A. scabra* with globiferous pedicellariae from *E. chloroticus* attached to the tube feet were encountered often in the field. This evidence gives no indication of the actual effectiveness of this response, and since the diet of *A. scabra* at Leigh consists almost entirely of *E. chloroticus* (Dr M.F. Barker, pers. comm.), it seems likely that it is of only limited value.

Daton *et al.* (1970, 1977) have demonstrated that the echinoids *Sterechinus neumayeri* and *Pseudechinus magellanicus* use layers of debris apparently to hide from predators. In this context, *E. chloroticus* often covers itself with shells, stones, algal fragments and sticks (Dix, 1970), and this covering (i.e. camouflage) habit may be a third type of defensive mechanism.

Dietary species tested, which were apparently insensitive to contact with *A. scabra*, were *Ischnochiton maorianus*, *Patelloida corticata*, *Zeacumantus* sp., *Turbo smaragdus*, *Buccinulum vitatum*, *Prototheca crassicosta* and *Siphonaria zelandica*. Of these, only *Zeacumantus* sp. has little or no spatial overlap with the seastar. The two non-dietary species tested, *Diloma arida* and *Haliotis virginea*, exhibited reactions identical with those of *Melagraphia aethiops* and *H. iris* respectively.

CHAPTER 7. SOME BIOTIC FACTORS AFFECTING DIETARY COMPOSITION IN *ASTROSTOLE SCABRA*

INTRODUCTION

The diet of carnivorous starfish is determined by interactions between a number of biotic factors including prey and predator size, prey availability, and prey-predator spatial overlap (Christensen, 1970; Menge, 1972b; Doi, 1976; Dayton *et al.*, 1977). The size of food ingested by asteroids with an intraoral mode of feeding is limited by the width of the mouth aperture (Christensen, 1970). In other seastars studied, prey size was shown to be independent of predator size (Paul and Feder, 1975; Dayton *et al.*, 1977), while in some seastars, predator size directly influences dietary composition such that larger individuals consume larger prey items. This shift of emphasis in prey size during ontogeny may be from small to large individuals within a single species (Birkeland, 1974; Doi, 1976; Ribi *et al.*, 1977), or from small to large specimens within different genera (Hancock, 1955; Feder, 1959; Mauzey, 1966; Birkeland *et al.*, 1971; Menge and Menge, 1974).

The concept that a prey species may achieve a refuge in size or space from predation has achieved prominence in recent considerations of intertidal community dynamics (see below). This aspect of predator-prey relationships in seastars was first introduced by Needler (1941) who noted that *Asterias vulgaris* must be 1.5 times the length of a prey oyster for an attack to be successful. Paine (1976), using the *Pisaster-Mytilus* interaction, found that large mussels were immune from predation by intertidal starfish of a given size, and below a certain minimum size, mussels were not eaten by large seastars. The importance

to a prey species of a size refuge from predation is that predator and prey can exist in close proximity. A prey species may attain a size refuge solely through growth (Connell, 1972), or through the enhanced efficiency of an escape response conferred on the individual by increased size (Feder, 1967).

Lewis (1964) considered that while predation did not set clear-cut limits to distribution in prey species, it could affect species abundance at a given level. However, it has been illustrated that the lower, vertical, intertidal limits of *Mytilus californianus*, *Perna canaliculus*, *Balanus cariosus* and *B. glandula* are very constant, and are maintained by predation (Connell, 1970; Dayton, 1971; Paine, 1971, 1974). Potential prey individuals lying above this lower vertical limit have a spatial refuge from predation, as they lie above the foraging range of most predators. The phenomenon by which predation restricts prey species to certain parts of their potential vertical range is a function of prey-predator spatial overlap. Although the examples given above are relatively clear-cut, less obvious interactions exist where predation does not entirely exclude a prey species from a particular intertidal stratum. At Mukkaw Bay, Washington, only the larger size classes of *Tegula funebralis* overlapped with *Pisaster ochraceous* and were reduced in number by 25-28% per year, but were not eliminated entirely from this portion of their range (Paine, 1969b). Of five *Acmaea* species studied by Feder (1963), *Acmaea scabra* was the limpet eaten most frequently by *P. ochraceous*, although it had little spatial overlap with the seastar. The absence of an escape reaction in this species was thought to account for its relatively frequent occurrence as a food item. Birkeland (1974) also demonstrated that a prey species may have a variety of partial refuges from predation.

The relative availability of different prey species and their sizes is a difficult parameter to measure, but is an important component

of any prey-predator interaction (Ivlev, 1961). The relative availability of starfish prey has been considered on both an "apparent" basis - where all spatially co-occurring prey are deemed available (Doi, 1976; Ribi *et al.*, 1977), and on an "actual" basis - where prey availability is determined as a derived function of predator foraging time, speed, size and feeding rate (Menge, 1972b).

The aims of the present study with *Astrostole scabra* were to determine if dietary composition, feeding frequency, and size of prey taken changed with an increase in size of seastar. Prey-predator spatial overlap and prey size were also examined to determine whether prey species attain a refuge in size or space from predation by seastars of a particular size.

MATERIALS AND METHODS

Arm length and/or wet weight have been regarded as reliable parameters of size in seastars (Feder, 1963; Hatanaka and Kosaka, 1959), but as wet weight and arm length in intertidal *A. scabra* are significantly correlated (Chapter 2), arm length alone was adopted as a single, stable criterion of size. The arm length (expressed as R) of all feeding (everted stomach) and non-feeding seastars encountered during the collection of data on dietary composition (Chapter 4) was measured from the proximal edge of the madreporite to the tip of the opposite arm when the ray was fully relaxed. This point was reached when the ray tip showed no abactinal flexure, and when light was visible through papular areas of the abactinal surface of the animal.

Prey items were retrieved from folds of the everted stomach, identified, counted and measured to the nearest 0.1mm with vernier calipers. Prey dimensions are expressed as anterior-posterior length for chitons, and shell height for spiral-shelled gastropods. These measurements represent the longest linear dimension of prey specimens,

and although seastars may assess prey suitability according to other criteria such as volume, strength of adhesion to substrate and excretory output, these probably increase with prey size.

Availability of prey species and their size-frequencies within the foraging range of *A. scabra* were determined by collecting and measuring specimens from study sites 1-4 in January, February, April, and May 1977, and July 1978. The upper limits of the foraging range of *A. scabra* were ascertained from general observations made between July 1975 and January 1977. Prey-predator spatial overlap patterns were delineated by counting and measuring all potential prey organisms occurring in four to ten 0.25 m^2 quadrats laid at 3m intervals along five transect lines from above the asteroids foraging range to ELWS. These data were accumulated at the same time as prey collections, and were derived from the same position within each study site at every visit.

Statistical methods

The monthly feeding frequency of individual *A. scabra* could not be determined because the residence period of specimens at any site was relatively short (Chapter 2). However, the data available allow a comparison of mean monthly feeding frequencies of seastars in different size classes within the intertidal population.

$$\text{The ratio:-}\ \frac{\text{Proportion of total feeders in size class A}}{\text{Proportion of population in size class A}}$$

(where A = any size class at all sites combined) provides an index of relative feeding frequency. When this ratio equals 1 the feeding frequency of the selected size class is equal to its abundance in the whole population; a ratio of >1 indicates high feeding frequency; and a ratio of <1 suggests low feeding frequency.

Dietary overlap (R_o) between seastar size classes was measured

according to Horn's (1966) equation:

$$R_o = \frac{(Hmax - Hobs)}{(Hmax - Hmin)} ,$$

where

$$Hmax = \sum_{i}^{s} \frac{xi}{X + Y} \log \frac{X + Y}{xi} + \frac{yi}{X + Y} \log \frac{X + Y}{yi} ,$$

$$Hmin = \frac{X}{X + Y} [H(X)] + \frac{Y}{X + Y} [H(Y)] ,$$

$$Hobs = H (X + Y) ,$$

$$H = -\sum_{i}^{p} pi \log_n pi$$

X = number of feeding seastars in size class X,

Y = number of feeding seastars in size class Y,

xi = proportion of species i in the diet of seastars in size class X,

yi = proportion of species i in the diet of seastars in size class Y,

pi = proportion of the ith species in the whole diet.

When $R_o = 0$, diets are completely distinct, and when $R_o = 1$, diets are identical with respect to proportional species composition.

The size-frequency distribution of spatially co-occurring (available) prey was compared with the size-frequency distribution of prey actually eaten by means of a chi-squared test for heterogeneity (Sokal and Rohlf, 1969).

The electivity (e) of seastars was evaluated following Ivlev (1961): $e = \frac{(ri - pi)}{(ri + pi)}$, where ri is the relative proportion of prey eaten, and pi is the relative proportion of prey available. Values of e between 0 and -1 indicate discrimination against that prey size class, and values of 0 to +1 indicate preferential feeding.

RESULTS

Effects of predator size on dietary composition and feeding frequency

Except in October and December 1976, the highest feeding frequency was shown by R = 10-30mm seastars (Fig. 7.1). The decline in the proportion of the intertidal population feeding during October and December (Fig. 4.4) was due to a reduction of feeding activity by animals in this size group. In contrast to other size classes, seastars of R = 50-70mm and R = 70-90mm displayed relatively little seasonal fluctuation in feeding frequency. Feeding activity in R = 10-30mm and 90-110mm size classes peaked in May and June.

Dietary composition altered qualitatively with increased predator size (Fig. 7.2, all sites combined). Two small rissoids, *Rissoina chathamensis* and *Estea* sp., and the eatoniellid, *Eatoniella* sp. constituted 46% of the diet of small (R = 10-20mm) seastars, whereas trochids and chitons formed only 10% of prey numbers. Everted stomachs accounted for another 24% of feeding records for seastars of this size. For the R = 20-30mm size class, rissoids and eatoniellids constituted only 27.3% of prey items, whereas chitons (15%) and trochids (16.4%) assumed a more significant numerical role. This trend was continued by *A. scabra* of R = 30-40mm, for which rissoids and eatoniellids contributed 2.6% of prey numbers only, and chitons 21%. The isopod *Exosphaeroma obtusum* (10.5%) achieved peak importance as a prey species for predators of this size. Rissoids and eatoniellids were a minor food of seastars above R = 30mm, and were not found in the diet of seastars of R >90mm. Chitons and trochids remained in the diet until seastars reached R >150mm and R >160mm respectively. The large turbinid *Turbo smaragdus* comprised 16.6% of prey numbers for seastars of R = 100-110mm, 43.7% for R = 110-120mm specimens, 22.2 - 33.3% for seastars of

FIGURE 7.1: Feeding frequency indices of *A. scabra* of various size classes from all study sites between January and December 1976.

A, R = 10-30mm; B, R = 30-50mm; C, R = 50-70mm; D, R = 70-90mm; E, R = 90-110mm

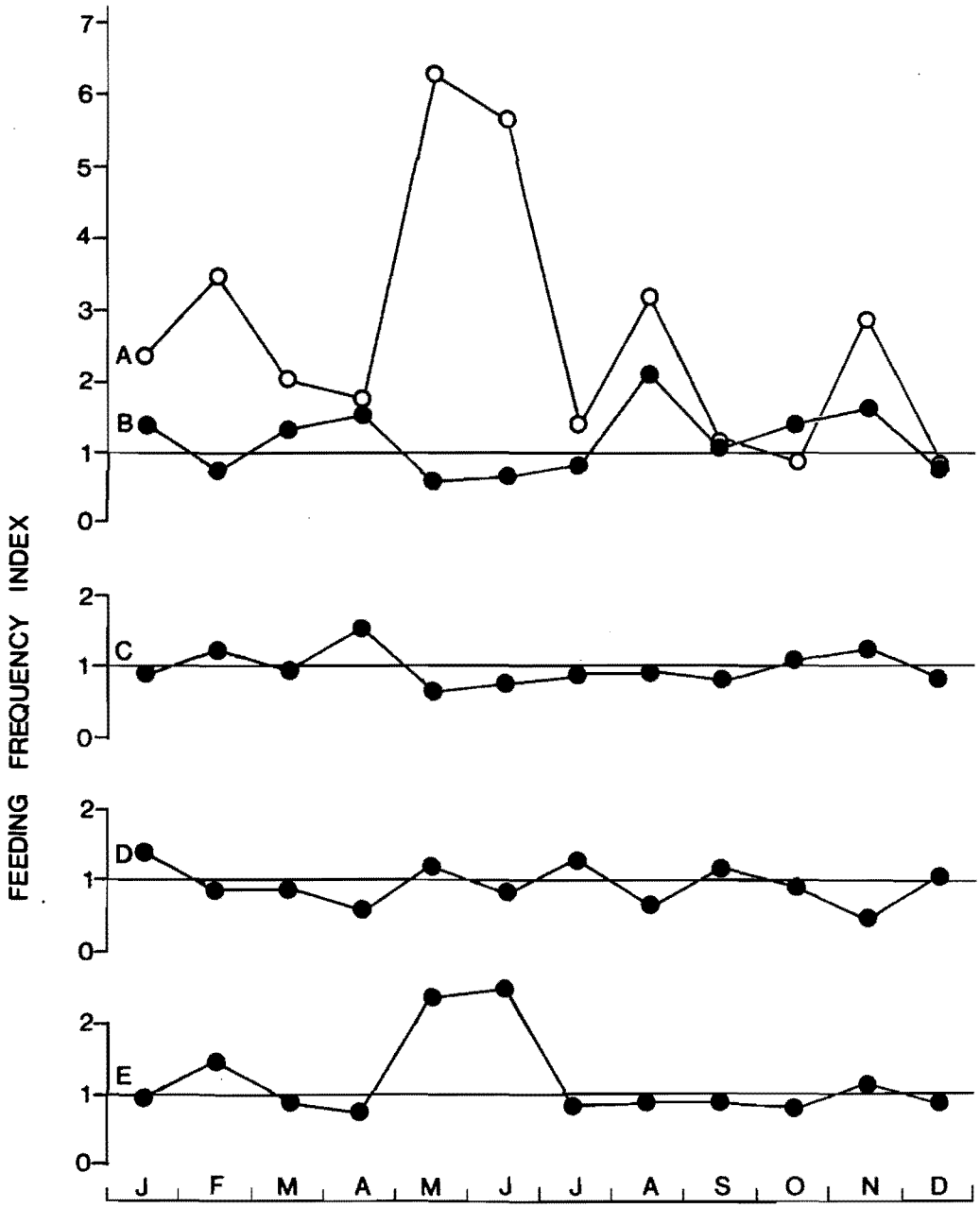
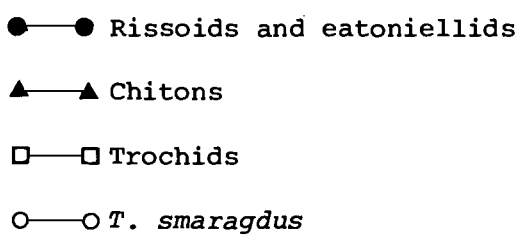
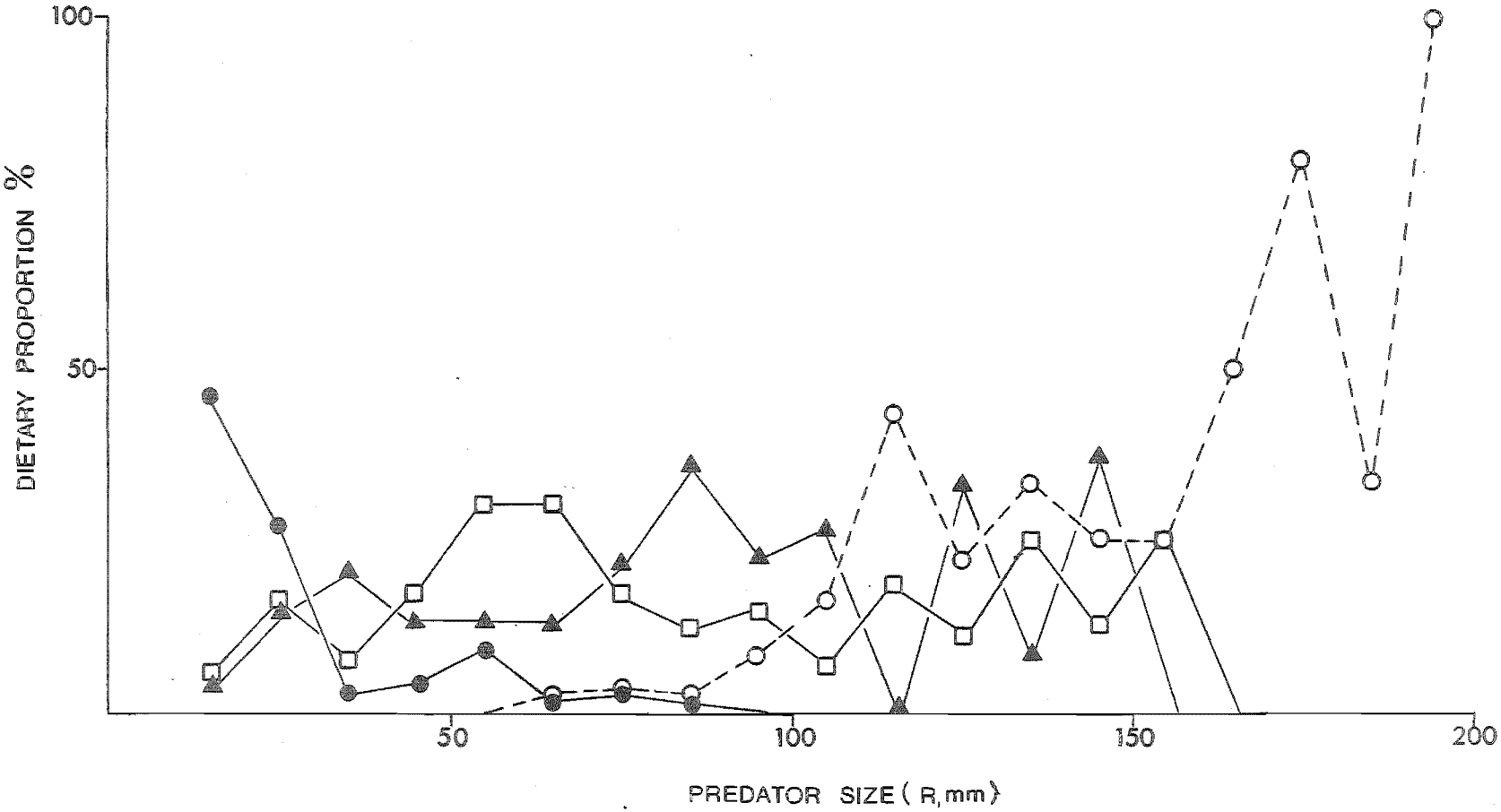

FEEDING FREQUENCY INDEX
7
6
5
4
3
2
1
0
A
B
C
D
E
J
F
M
A
M
J
J
A
S
O
N
D

FIGURE 7.2: Qualitative changes in dietary composition with increase in predator size, all sites combined. (Prey items expressed as percentage of all prey in diet.)




100
50
DIETARY PROPORTION %
50
100
150
200
PREDATOR SIZE (R, mm)

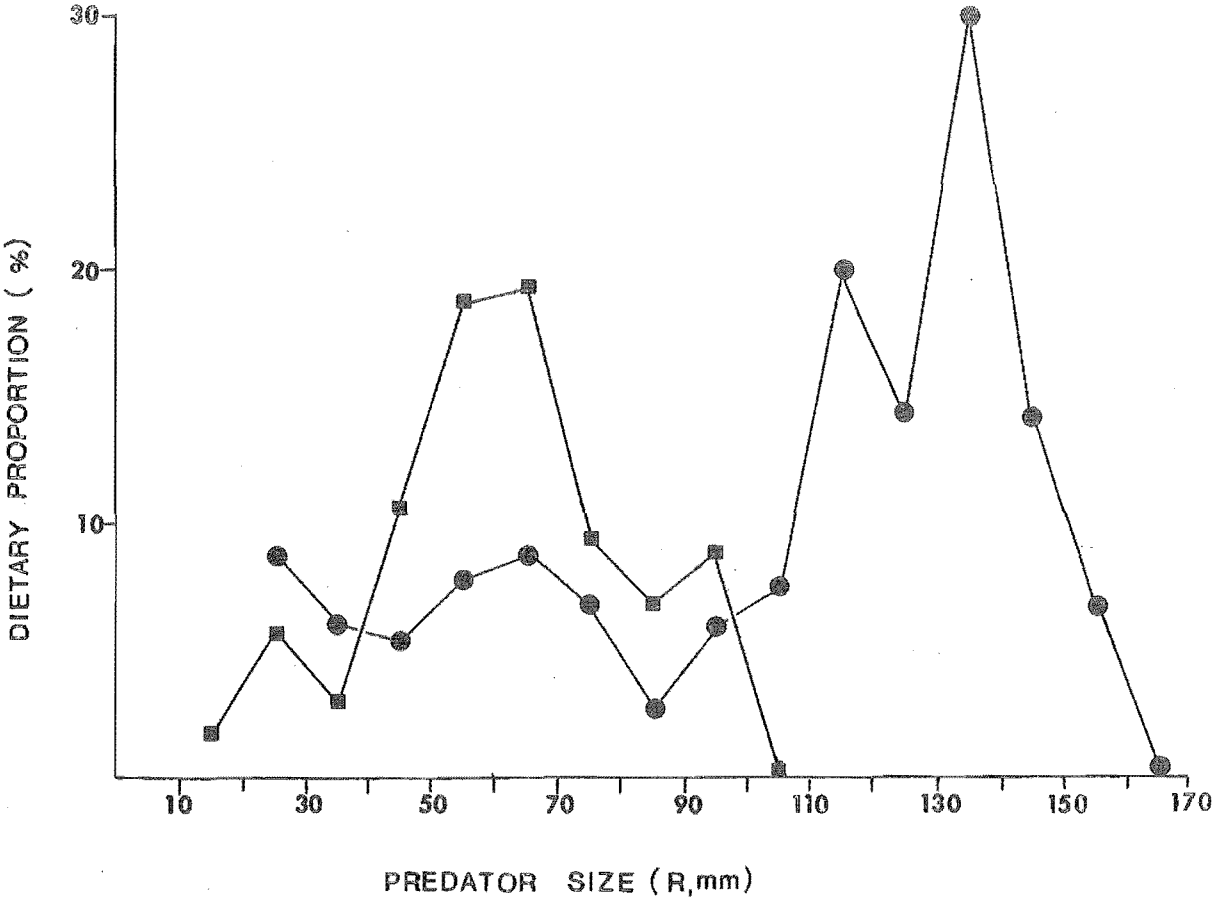
R = 120-160mm, and 33.3 - 100% for seastars of R >160mm. Everted stomach records and various Decapoda made up the remaining components of the diet of these large starfish.

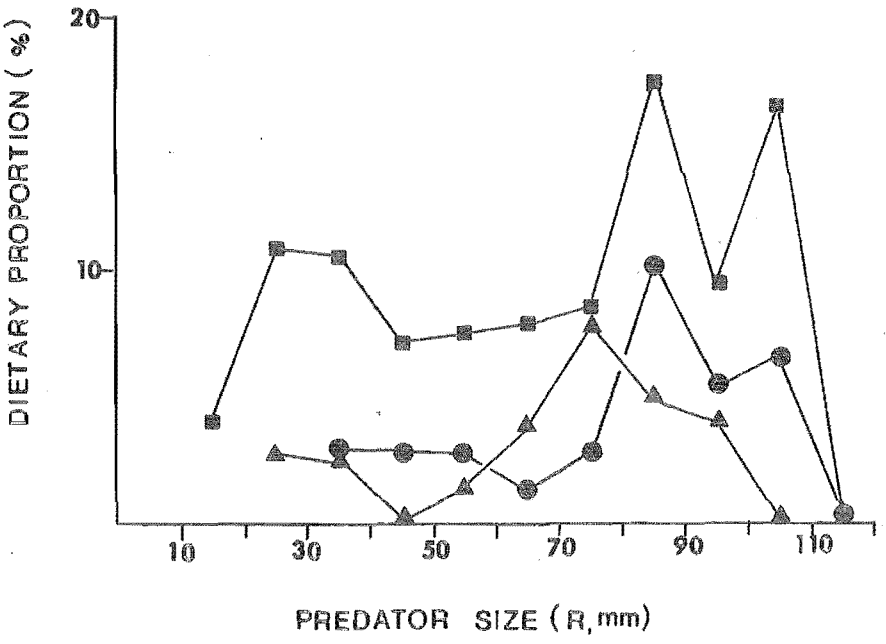
Not only did gross dietary composition alter with an increase in predator size, but the relative proportions of species within a given higher taxonomic group also changed. Thus, *Micrelenchus dilatatus* was the most numerous of four trochids in the diet of seastars up to R = 100mm, but larger seastars fed on only one trochid, *Melagraphia aethiops* (Fig. 7.3). *Ischnochiton maorianus*, *Onithochiton neglectus* and *Amaurochiton glaucus* appeared progressively in the diet as seastar size increased, making their initial dietary contributions at R = 10-20mm, R = 20-30mm, and R = 30-40mm respectively (Fig. 7.4). *I. maorianus* was the dominant chiton prey and accounted for 4.0 - 17.5% of all prey items in seastars of up to R = 110mm. *O. neglectus* achieved relative numerical importance only for *A. scabra* of R = 60-80mm, after which it again became the least numerous chiton in the diet and disappeared at R = 100mm. With the exception of a few scattered records, *I. maorianus* and *A. glaucus* were absent from the diet of *A. scabra* of R >110-120mm. Chitons comprised 36.2% of prey items and were the prime food source for *A. scabra* of R = 80-90mm. Chitons predominated over trochids in the diet of seastars in the 70-110mm classes.

The summary given above indicates five shifts in dietary composition as *A. scabra* increased in size. The first occurred at R = 30-40mm when rissoids and eatoniellids all but disappeared from the diet and were replaced by chitons, trochids and isopods. A second dietary shift was reached at R = 40-70mm when *M. dilatatus* became the single most numerous prey species. At R = 70-110mm chitons predominated, whereas at R = 100-110mm *M. aethiops* and *T. smaragdus* were the most numerous prey species. Finally, at R >160mm, *T. smaragdus* formed up to

FIGURE 7.3: Per cent inclusion of *M. aethiops* (●, n = 61) and *M. dilatatus* (■, n = 88) in the whole diet according to seastar size.

FIGURE 7.4: Per cent inclusion of *I. maorianus* (■, n = 80), *O. neglectus* (▲, n = 29), and *A. glaucus* (●, n = 28) in the whole diet according to seastar size.


30
20
10
DIETARY PROPORTION (%)
10
30
50
70
90
110
130
150
170
PREDATOR SIZE (R,mm)

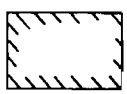

20
10
DIETARY PROPORTION (%)
10
30
50
70
90
110
PREDATOR SIZE (R,mm)

100% of the diet.

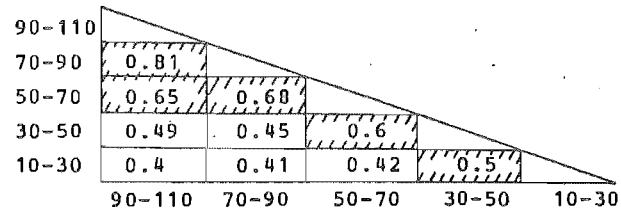
Although diet changed with increasing seastar size, some predators within different size classes still had diets which overlapped in terms of species composition. For example, overlap statistics for site 1 indicated that with the exception of the interaction between R = 50-70mm and R = 90-110mm, animals in adjacent size groups had a large degree of overlap in dietary composition, whereas non-adjacent size classes had comparatively less pronounced overlap (Fig. 7.5). The pattern at site 2 was the same, except that overlap between the R = 30-50mm and R = 50-70mm size classes, and also between the R = 10-30 and 30-50mm groups was reduced to less than 50%. Site 3 was the only locality where R_o <50% between R = 50-70 and 90-110mm, and between R = 70-90 and 90-110mm size classes, but the R = 10-30mm group had 63% overlap with the R = 50-70mm portion of the population. R = 30-50mm animals had 54% overlap with R = 70-90mm specimens. At site 4, all size classes except R = 10-30mm had more than 50% overlap with each other in dietary composition. Dietary shifts were therefore incomplete, and the change in diet with increase in seastar size was restricted to certain portions of the whole diet. As seastar density, wave exposure, and nature of substrate were similar at all localities studied, it is likely that the type, density, and proportional composition of the prey community largely determined the degree to which the diets of differently sized seastars overlapped.

Increase in seastar size was correlated directly with an increase in the mean size of spiral-shelled gastropods and chitons consumed (Fig. 7.6). The reduction in mean size of chitons consumed when R = 50-70mm was caused by a decline in the numbers of *A. glaucus* in the diet, and increased proportions of the smaller *I. maorianus* and *O. neglectus* (Fig. 7.4). The mean size of chitons and spiral-shelled

FIGURE 7.5: Indices of prey species diversity (H, outside matrices) and similarity (R_o, inside matrices) of prey species composition of diets of different size classes of *A. scabra* at sites 1 (A), 2 (B), 3 (C), 4 (D), and at all sites combined (E). Mean R_o of each size class compared with all other size classes is also given. Everted stomach records omitted.

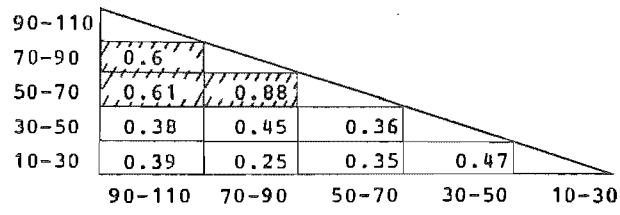
 $R_o \geq 0.5$

A



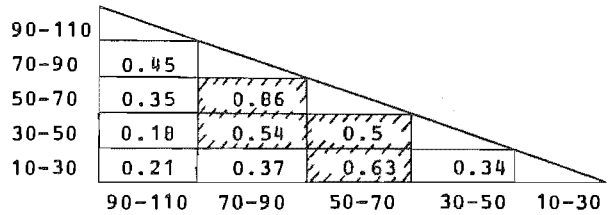
	90-110	70-90	50-70	30-50	10-30
n	29	50	51	18	45
H	2.4	2.6	2.8	2.5	2.5
mean R_o	0.58	0.58	0.58	0.51	0.43

B



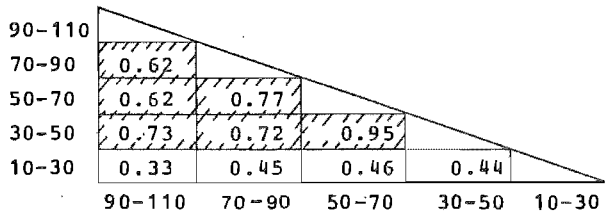
	90-110	70-90	50-70	30-50	10-30
n	15	33	38	7	4
H	1.8	2.4	2.2	1.5	1.0
mean R_o	0.49	0.54	0.55	0.41	0.36

C



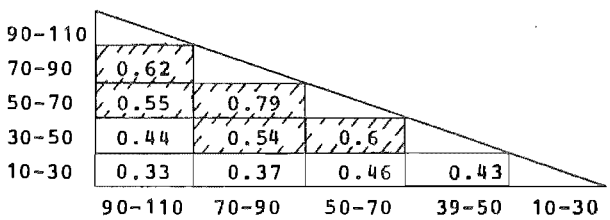
	90-110	70-90	50-70	30-50	10-30
n	5	32	54	10	14
H	1.6	2.3	2.4	1.0	2.2
mean R_o	0.29	0.55	0.58	0.39	0.38

D



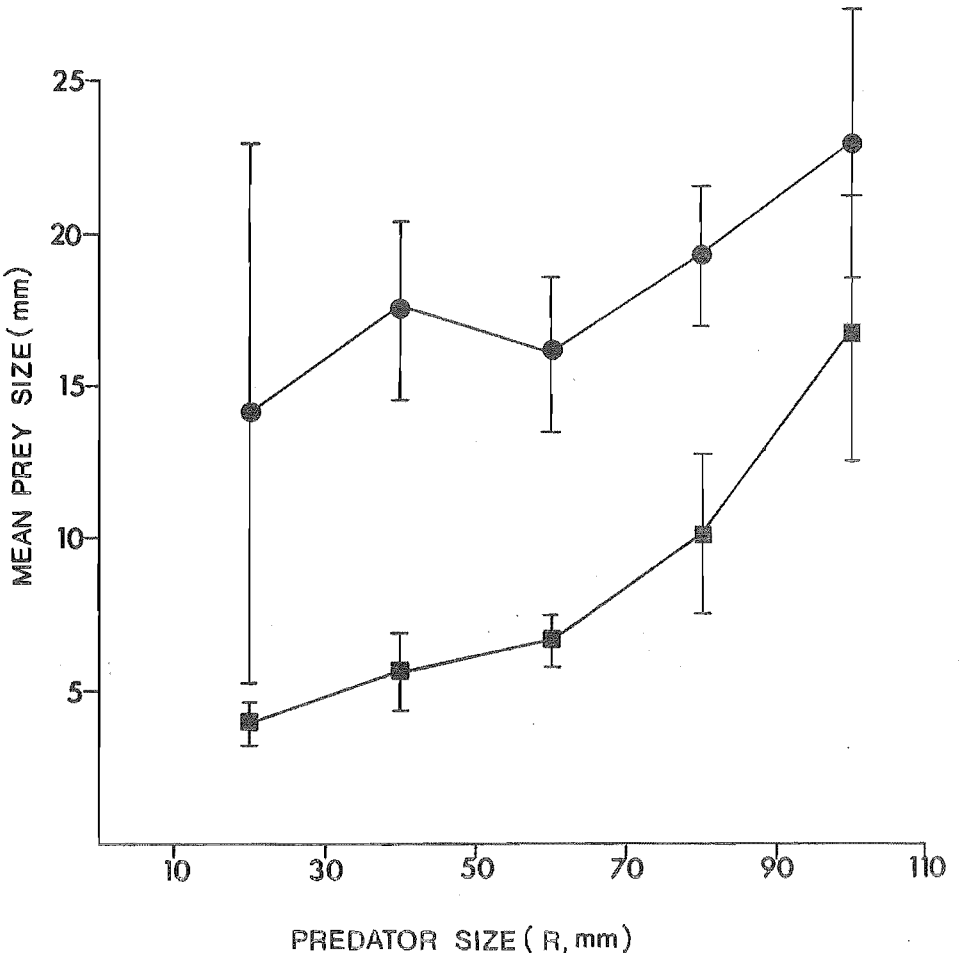
	90-110	70-90	50-70	30-50	10-30
n	11	22	27	26	11
H	2.0	2.2	2.1	2.3	1.6
mean R_o	0.57	0.64	0.7	0.71	0.42

E



	90-110	70-90	50-70	39-50	10-30
n	60	137	170	61	74
H	1.9	2.3	2.3	1.8	1.8

FIGURE 7.6: Relationship between mean size of chitons (●) and spiral-shelled gastropods (■) consumed, and seastar size.
(Vertical bars represent 95% confidence limits.)


25
20
15
10
5
MEAN PREY SIZE (mm)
10
30
50
70
90
110
PREDATOR SIZE (R, mm)

prey eaten by seastars of any size class was significantly different from that of any other size class (Figs 7.7, 7.8). Similarly, the mean sizes of chitons and spiral-shelled gastropods consumed by any single seastar size class were significantly different from each other (Table 7.1). Therefore, there was little dietary overlap between seastar size classes for chitons or spiral-shelled gastropods on the basis of prey size. Prey within these broad categories were partitioned amongst seastars partly according to species, and more completely according to size. In terms of the longest linear dimension, chitons eaten by seastars of a given size were larger than spiral-shelled prey, and therefore would appear to be easier to catch. The progressive inclusion of *I. maorianus*, *O. neglectus* and *A. glaucus* in the diet of *A. scabra* as the predator increased in size does not reflect increased nutritional requirements, as all three chiton species possess similar dry weight-shell length ratios (Fig. 7.9). More consumable biomass is provided by *M. aethiops* of comparable longest linear dimension (Fig. 7.10), and *T. smaragdus* yield twice the consumable biomass provided by chitons of the same size (Fig. 7.10). The dietary shift at R = 100-110mm to a diet composed chiefly of *M. aethiops* and *T. smaragdus* probably occurs because seastars of this size are now able to catch these prey. A consequence of this shift is that more biomass is available per capture, and so provides more potential food per meal for larger predators with their increased nutritional requirements. Small *A. scabra* compensate, to some extent, for the small size of their prey by consuming more than one item per meal (Fig. 7.11) and by feeding more frequently than larger specimens (Fig. 7.12).

Significant positive correlations were found also between the size of *A. scabra* and the size of some individual prey species consumed. The relationship between the size of *A. scabra* and both *M. aethiops* and

TABLE 7.1. Difference in mean size (Mann-Whitney U test) of prey chitons and spiral-shelled gastropods consumed by *A. scabra* of single size classes. ($p < 0.05$ for all values).

SEASTAR SIZE CLASS (mm)	SPIRAL-SHELLED PREY (NO.)	MEAN SIZE (mm) (± SD)	CHITON PREY (NO.)	MEAN SIZE (mm) (± SD)	U VALUE
10-30	69	3.76 (± 2.53)	10	13.2 (± 9.4)	630
30-50	35	6.17 (± 4.15)	16	17.6 (± 5.6)	519
50-70	129	6.64 (± 2.72)	36	16.0 (± 7.7)	7 974
70-90	62	10.71 (± 10.8)	57	19.2 (± 5.1)	3 857
90-110	29	19.21 (± 10.6)	25	23.3 (± 11.0)	1 004

TABLE 7.2. Size related prey characteristics compared with prey density, escape reactions and predator preferences.

		I. maorianus	*A. neglectus*	*A. glaucus*
	Frequency in whole diet (%)	8.8	3.1	2.9
	Mean size consumed (mm)	15.3	19.4	26.8
	Mean size Predator (R, mm) (± S.D.)	64.1 (±25.2)	70.5(±21.8)	(76.6 (±21.1)
	Attract. threshold for mean size pred. (mm)	6.2	9.3	12.2
	Prey size refuge from mean sized predator (mm)	27	31.0	33.7
*1	$\frac{\text{Size ref. from mean pred. (mm)}}{\text{Mean size eaten (mm)}}$	1.7	1.6	1.2
	Mean pred./prey size ratio	4.2	3.6	2.8
	Escape reaction	No	Yes	Yes
	Abundance (no./m^2)	14.3	1.0	1.29
*2	Predator preference	1	3	2
	Mean no. eaten/meal	1.3	1.1	1.0
	% prey population below size ref. from mean sized predator	94	93	91
	Breadth of prey sizes available to mean sized seastar (mm)	20.8	22.0	21.5

*1 As this value approaches 1, the prey eaten is closer to its size refuge from a mean sized predator on this species.

*2 Arbitrary units.

FIGURE 7.7: Difference in mean size (Mann-Whitney U test, values in body of matrix) of spiral-shelled prey gastropods consumed by *A. scabra* of given size classes (outside matrix).
n = sample size ($p < 0.05$ for all values).

FIGURE 7.8: Difference in mean size (Mann-Whitney U test, values in body of matrix) of prey chitons consumed by *A. scabra* of given size classes (outside matrix).
n = sample size ($p < 0.05$ for all values).

90-110					
70-90	9278.5				
50-70	2913	8006.5			
30-50	10134	1416.5	3598		
10-30	1765.5	4963	7329	1819.5	
	90-100	70-90	50-70	30-50	10-30
n	29	62	129	35	69

90-110					
70-90	6558				
50-70	4941	5713			
30-50	3864	4310.5	3706		
10-30	2978	3355	3181	3029	
	90-110	70-90	50-70	30-50	10-30
n	25	57	36	16	10

FIGURE 7.9: Relationship between shell length (including girdle) and dry weight of foot and viscera in *I. maorianus* (■), *O. neglectus* (●), and *A. glaucus* (▲).

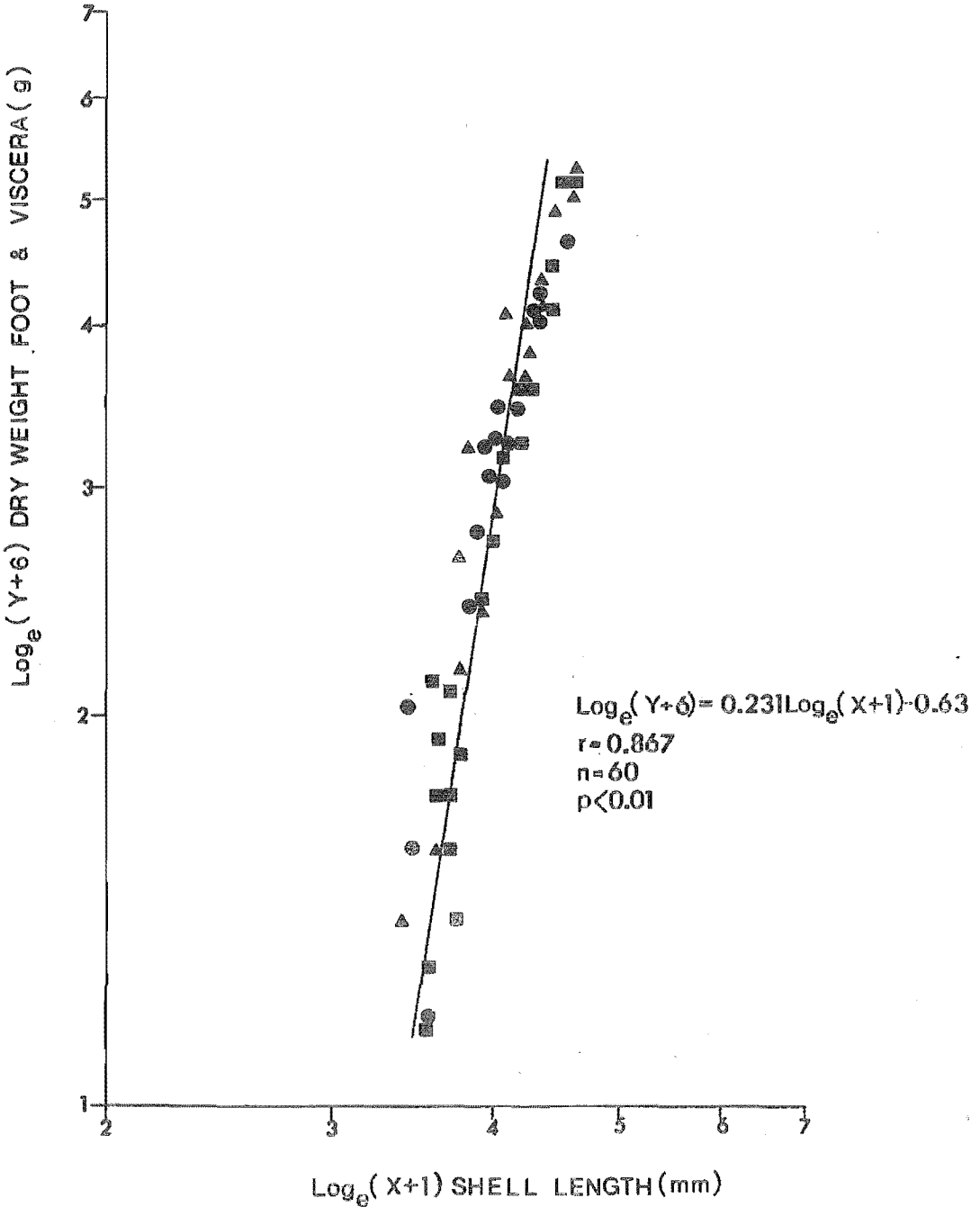

Log$_e$(Y+6) DRY WEIGHT FOOT & VISCERA (g)
Log$_e$(X+1) SHELL LENGTH (mm)
Log$_e$(Y+6)= 0.231Log$_e$(X+1)-0.63
r= 0.867
n=60
p<0.01

FIGURE 7.10. Relationship between shell height and dry weight of foot and viscera in *M. aethiops* (■) and *T. smaragdus* (●).

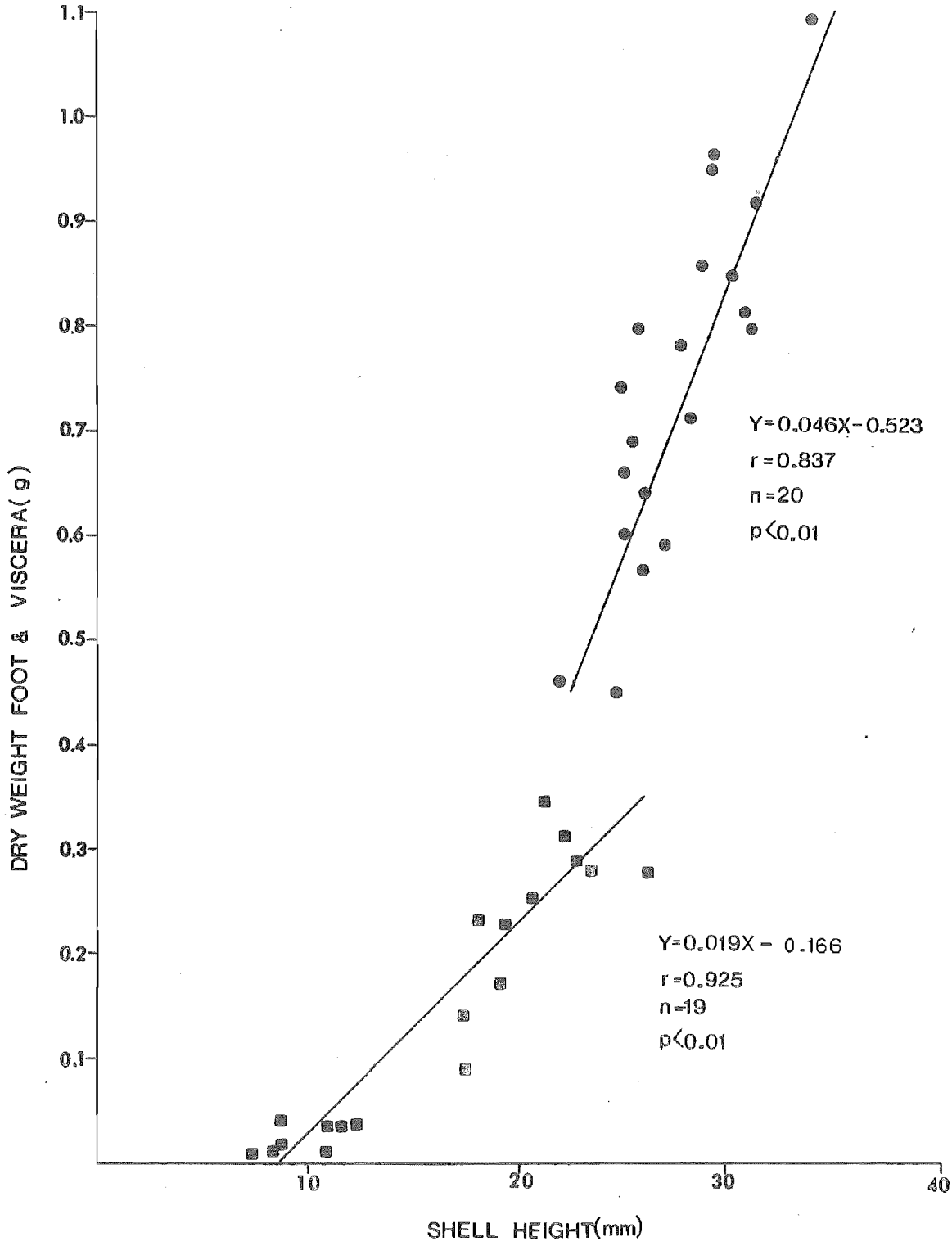
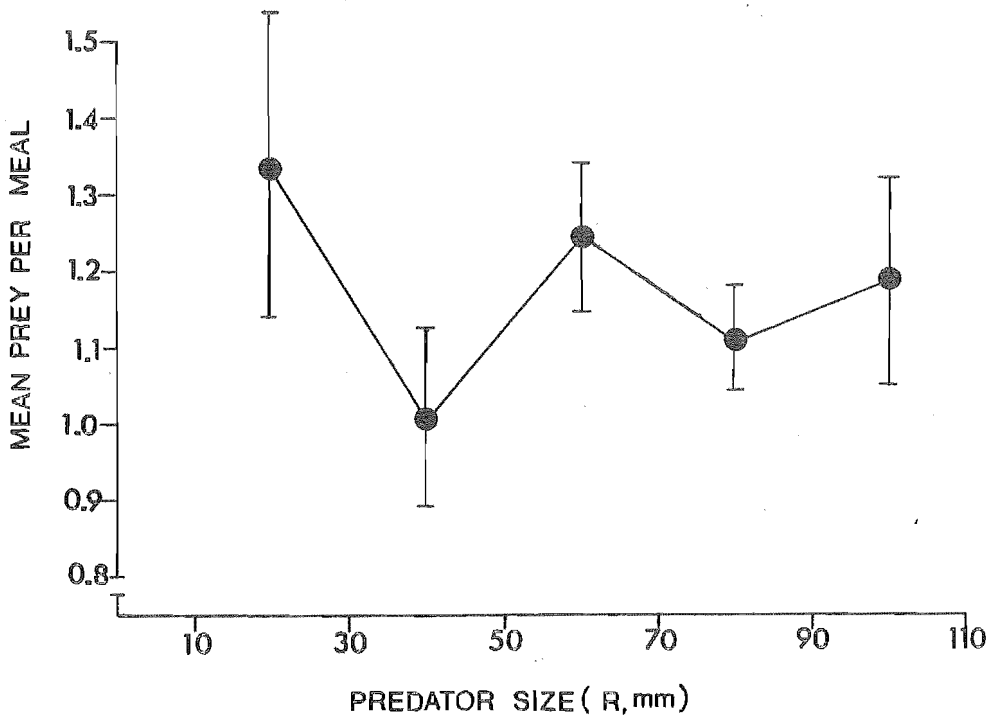
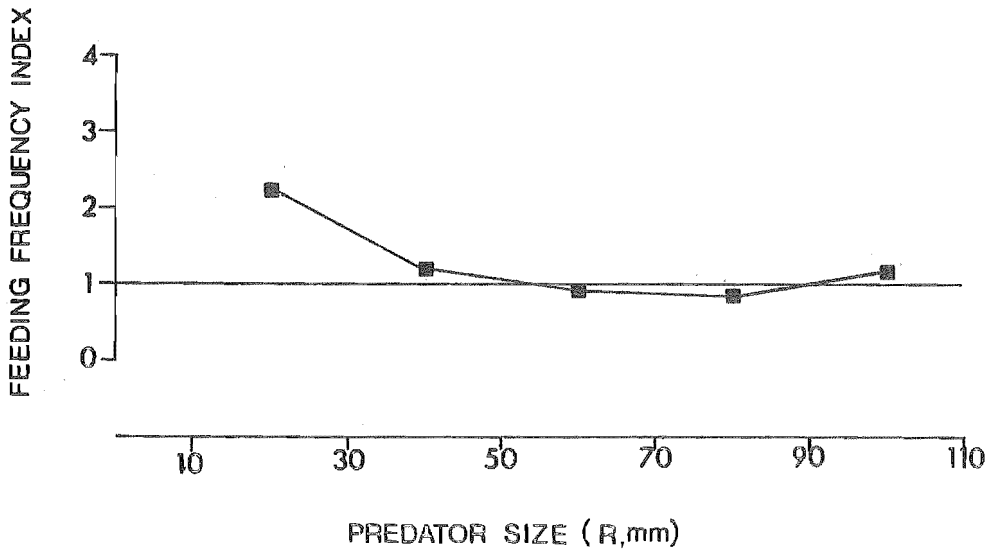

DRY WEIGHT FOOT & VISCERA(g)
SHELL HEIGHT(mm)
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
10
20
30
40
Y=0.046X-0.523
r=0.837
n=20
p<0.01
Y=0.019X - 0.166
r=0.925
n=19
p<0.01

FIGURE 7.11: Mean prey per meal consumed by *A. scabra* of different size classes.

R = 10-30mm *A. scabra* ate more than one item per meal significantly more often than all other size classes (Mann-Whitney U test, U = 3542, 3897, 4082 and 4211 respectively, n = 75, 199, 173 and 75 respectively). ($p < 0.01$ for all values).

FIGURE 7.12: Mean annual feeding frequency of different *A. scabra* size classes from all study sites between January and December 1976.


MEAN PREY PER MEAL
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
10
30
50
70
90
110
PREDATOR SIZE (R, mm)


FEEDING FREQUENCY INDEX
4
3
2
1
0
10
30
50
70
90
110
PREDATOR SIZE (R, mm)

T. smaragdus prey (Fig. 7.13) shows that larger seastars caught larger snails. The capture and pursuit of *M. aethiops* is therefore a function of both prey and predator sizes. The prey size component is a combination of size and escape behaviour, and the success of the escape reaction therefore, at least in part, is dependent on the prey size/ predator size ratio. *I. maorianus* has no escape response (Chapter 6), and the relationship between the size of *A. scabra* and *I. maorianus* prey (Fig. 7.14) therefore, is not affected by such behaviour. Otherwise, the factors underlying this relationship are identical to those pertaining in the *A. scabra* - *M. aethiops* interaction. No clear relationship existed between seastar size and the size of prey *M. dilatatus*, *A. glaucus* or *O. neglectus*.

Effect of prey size on dietary composition

The persistent co-occurrence of prey and predator can occur if potential prey species, in the absence of heavy exploitation, are able to attain a size refuge or if a combination of size and escape reactions provides a refuge. There has been no attempt to quantify the point at which particular prey species attain a refuge in size from predation by particular seastars, or the point at which they become liable to predation by seastars. Knowledge of the relationship between seastar size and prey size permits the determination of both the "attractiveness threshold" i.e. the size at which predation commences, and the upper maximum size limit (size refuge) beyond which a prey species cannot be eaten by seastars of a particular size. These parameters can be employed in the interpretation of dietary composition, and can explain why some potential prey items are absent from the diet.

An [illegible] relationship exists between the type and size of prey in a seastar's diet. The rissoids and eatoniellids which comprised a large portion of the diet of R = 10-30mm seastars, were very much

FIGURE 7.13: Relationship between prey size and predator size for *M. aethiops* (A) and *T. smaragdus* (B).

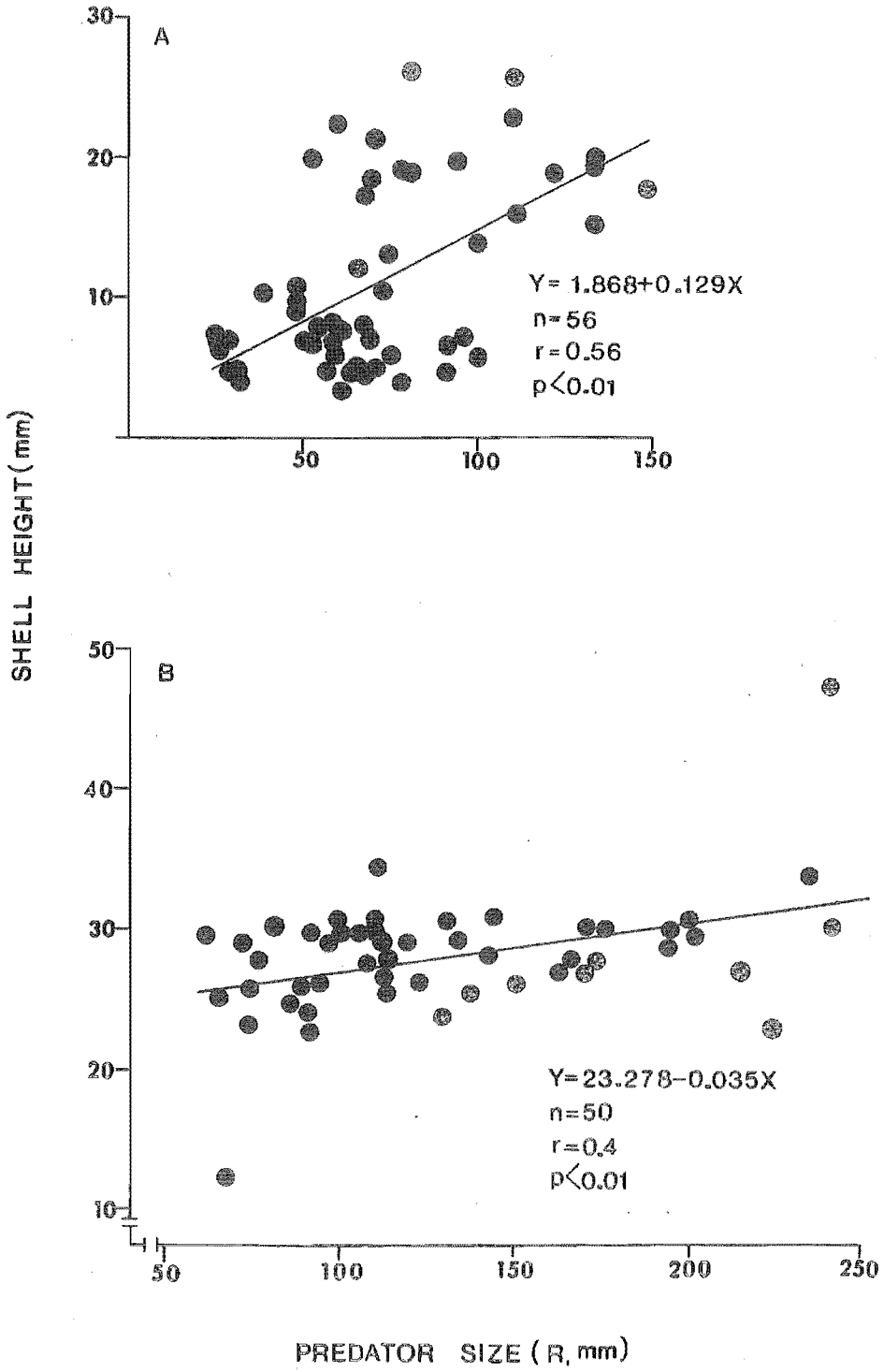
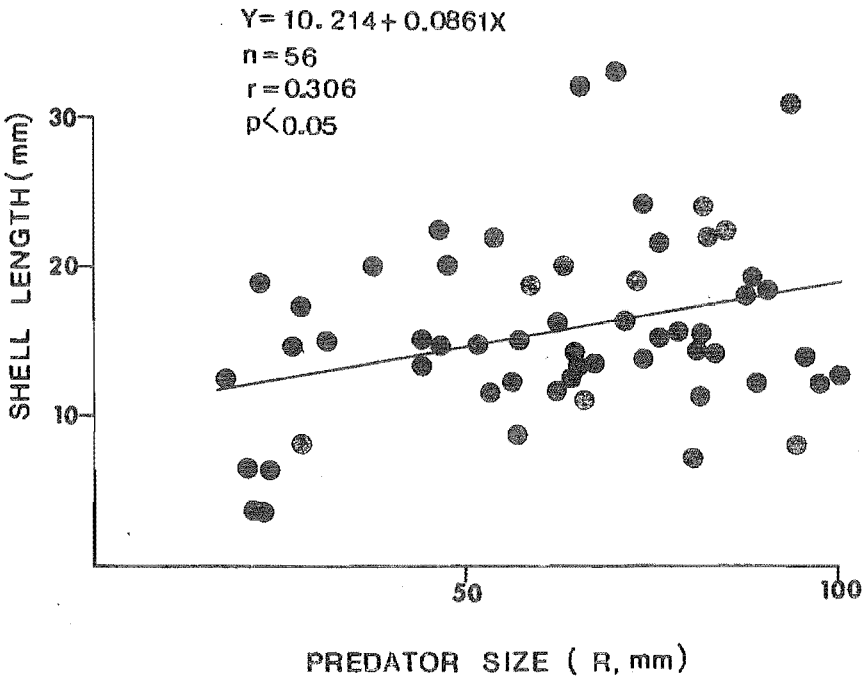

A
Y= 1.868+0.129X
n=56
r=0.56
p<0.01
B
Y=23.278-0.035X
n=50
r=0.4
p<0.01
SHELL HEIGHT (mm)
PREDATOR SIZE (R, mm)

FIGURE 7.14: Relationship between prey size and predator size for *I. maorianus*.

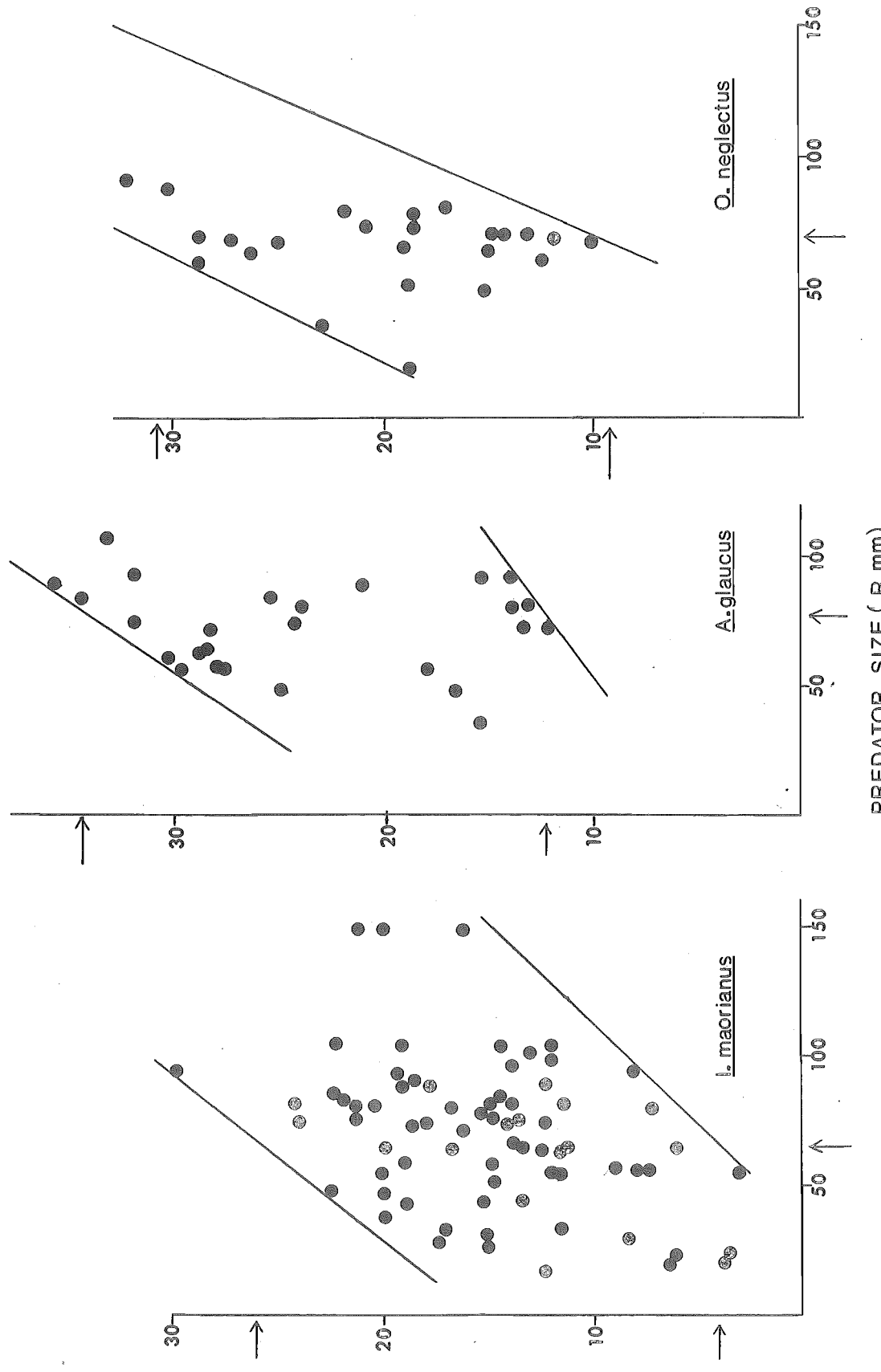

Y= 10. 214+ 0.0861X
n=56
r=0.306
p<0.05
SHELL LENGTH (mm)
30
20
10
50
100
PREDATOR SIZE (R, mm)

smaller than *T. smaragdus* which was an important component in the diet of large *A. scabra*. This prey/predator relationship was probably the outcome of interplay between the nutritional requirements of the predator, its ability to overwhelm prey of a certain size, and the relative availability of potential prey items of different sizes.

When size of *I. maorianus*, *O. neglectus* and *A. glaucus* prey was plotted against seastar size, lines fitted to the upper and lower size limits could be used to delineate the attractiveness threshold and size refuge characteristics respectively of the prey species (Fig. 7.15). The size refuge boundary cannot, however, reveal whether its configuration is due to prey size alone or also to escape behaviour. Similar problems arose when attempting to interpret factors determining the attractiveness threshold line. These limitations notwithstanding, it was possible to compare the attractiveness thresholds and size refuges for these three prey species and to assess their impact on dietary composition.

Size refuge and attractiveness limits for the three chiton species formed an ascending series in the order *I. maorianus*> *O. neglectus*> *A. glaucus* (Table 7.2, Fig. 7.15). Increases in attractiveness and size refuge limits of a prey species led to an increase in the mean size of seastars preying upon that species, and vice versa. Further, increases in these limits caused an increase in the mean size of chiton consumed, a decline in the mean number consumed per meal, and a decline in the frequency with which the prey appeared in the diet (Table 7.2). It is noteworthy that despite different size refuge and attractiveness limits, the size range of potential prey available to seastars was similar for all chiton species. Relative prey catchability, as measured by the mean predator size/mean prey size ratio was, in order of difficulty, *I. maorianus*< *O. neglectus*< *A. glaucus* (Table 7.2). *I. maorianus*, the preferred food of *A. scabra*,

FIGURE 7.15: Size refuge (upper) and attractiveness threshold (lower) limits for three major chiton prey species. Mean predator size and respective size refuge and attractiveness limits are indicated by arrows.


PREY LENGTH (mm)
30
20
10
I. macrianus
A.glaucus
O. neglectus
50
100
150
PREDATOR SIZE (R, mm)

was the most abundant chiton, had no escape reaction, had the largest proportion of its population below the size refuge limit for mean sized predators, and was easiest to catch. Thus, this chiton species was more available to *A. scabra* than either *O. neglectus* or *A. glaucus*. The mode of prey dispersion and the effective time the prey is exposed to the predator during one tidal cycle were the same for all chiton species (see below).

Effect of prey-predator spatial overlap on dietary composition

Spatial refuges from predation are sometimes obvious as when prey species occupy a zone at the top of a rocky shore which lies beyond the foraging range of predators. These situations require that the prey species' ability to withstand environmental extremes surpasses that of the potential predator.

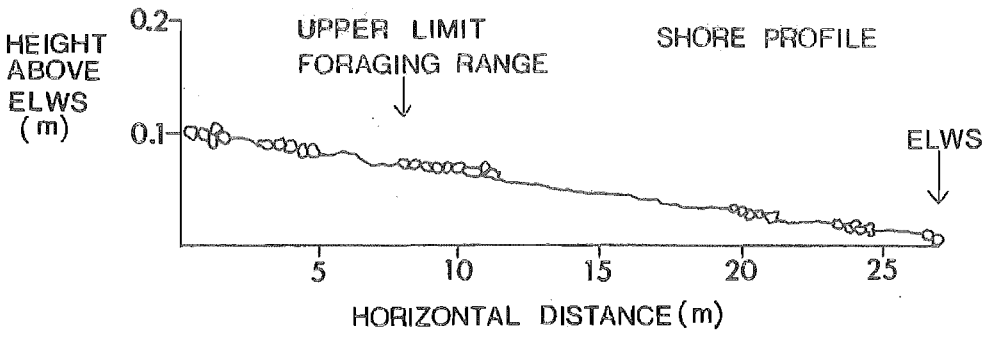
Prey removal rates based on population density measurements (Chapter 4) may give only a partial picture of relative prey availability. Some dietary species may be less available if, for example, the majority of their numbers lie at the upper end of a seastar's foraging range and are covered by water for less time during one tidal cycle than another prey species. Juvenile and adults of a single prey species might inhabit different strata within the intertidal zone, and this could influence the sites of prey consumed as those occurring lower on the shore would be exposed to foraging seastars for longer periods.

The interpretation of dietary composition in *A. scabra* must take into account the distribution of potential prey organisms within the intertidal zone. Sampling along transects connecting ELWS to the upper end of the seastar's foraging range, as done in this study, can clarify some aspects of relative prey availability but still provide some problems. Thus, data obtained in this manner represent prey

distributions at only one time and take no account of temporal variability in prey numbers or in the size-frequency characteristics of the population. Most prey were distributed patchily (Table 4.9, Chapter 4), and although a species may be present at a locality it may not occur on a random transect. In other words, rare or contagiously distributed species in particular are likely to be misrepresented numerically. Another problem is that the distribution of prey exposed during low tidal periods may not be indicative of their high tidal distribution, at which times most organisms feed and forage. Some prey may occur only in positions inaccessible to the observer, for example, on the undersides of very large boulders. The flat, bench-like profile of the shore at Kaikoura, and the presence of large, low tidal pools in the areas surveyed, could have led, in some cases, to distribution patterns lacking distinct vertical separation of potential prey species. Despite these potential shortcomings in sampling procedure, it should be noted that the majority of prey species are slow moving, are not restricted to inaccessible sites (pers. obs.), and did not appear to have pronounced seasonally variable densities (R. Rasmussen, 1965).

Vertical distribution patterns of prey differed at each site (Figs 7.16, 7.17, 7.18) but some general trends were clear. The very heterogeneous nature of site 2, with its large bedrock protrusions and extensive tidepools, made the area unsuitable for transect techniques. Here, the prey assemblage was similar to that of site 3, except for the absence of *R. varia* and a higher density of *M. dilatatus*. Although *T. smaragdus* occurred at sites 1 and 3, it was abundant only at site 1 where it constituted the major prey species. At both localities smaller specimens had less spatial overlap with *A. scabra* than large individuals. Except at site 1, where *O. neglectus* and *A. glaucus* were sparsely distributed and had little overlap with the

FIGURE 7.16: Vertical distribution and mean density patterns of major prey species at site 1. (Figures at intervals in prey distribution patterns are prey size range at that stratum.)


HEIGHT ABOVE ELWS (m)
0.2
0.1
UPPER LIMIT FORAGING RANGE
SHORE PROFILE
ELWS
5
10
15
20
25
HORIZONTAL DISTANCE (m)

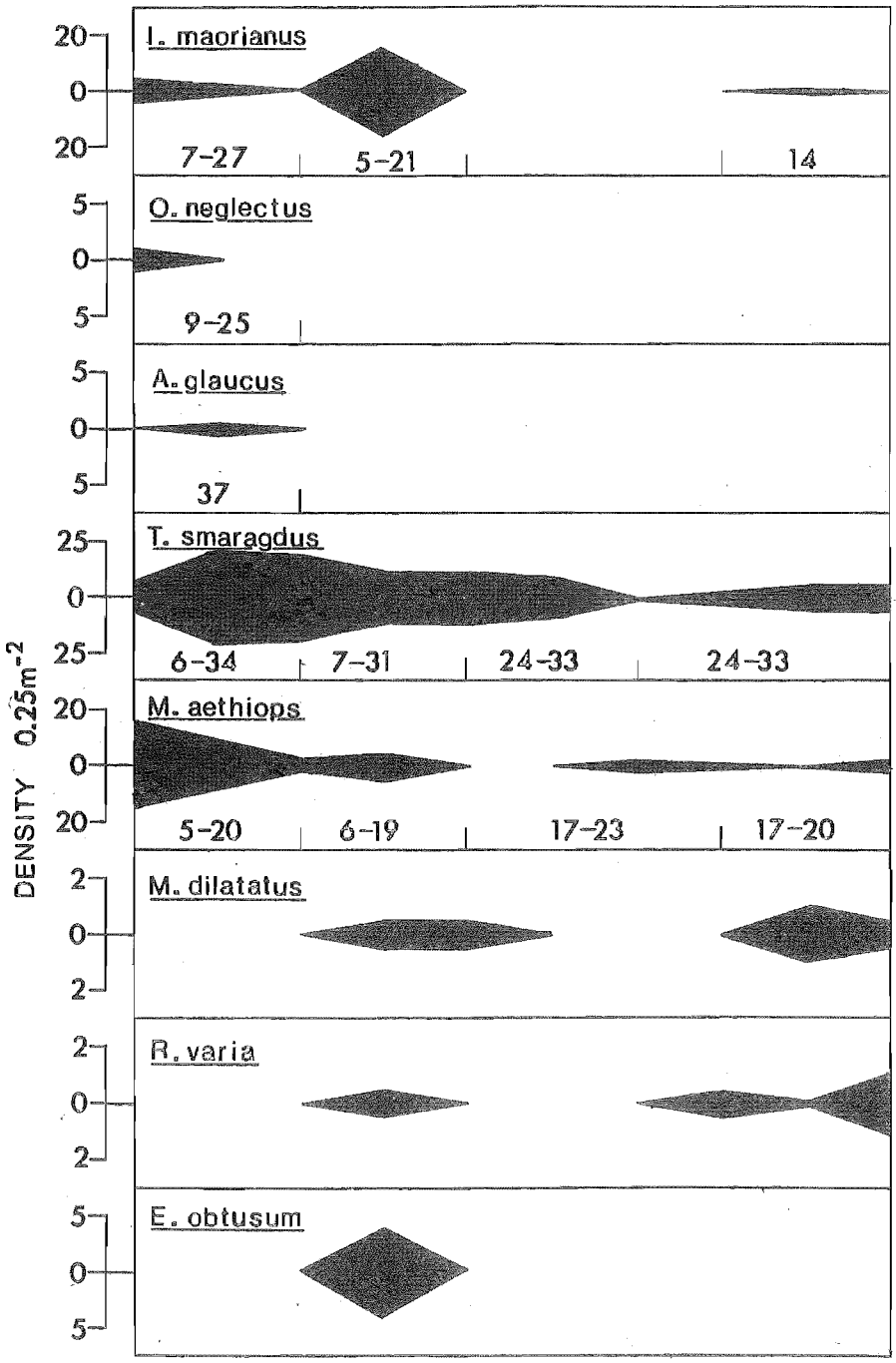
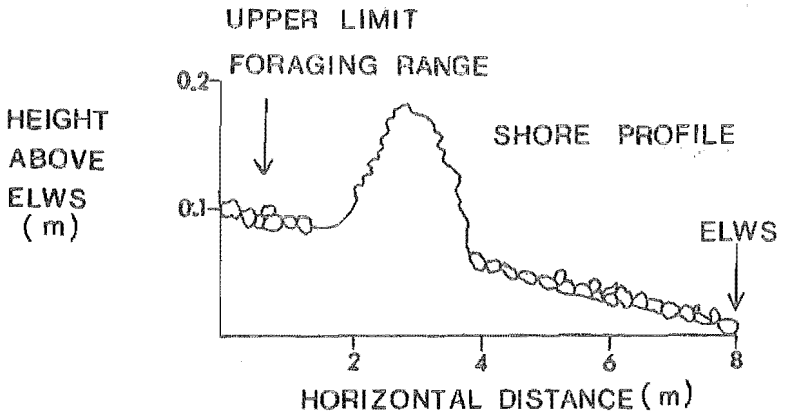

DENSITY 0.25m-2
I. maorianus
7-27
5-21
14
O. neglectus
9-25
A. glaucus
37
T. smaragdus
6-34
7-31
24-33
24-33
M. aethiops
5-20
6-19
17-23
17-20
M. dilatatus
R. varia
E. obtusum

FIGURE 7.17: Vertical distribution and mean density patterns of major prey species at site 3. (Figures at intervals in prey distribution patterns are prey size range at that stratum.)


UPPER LIMIT
FORAGING RANGE
HEIGHT ABOVE ELWS (m)
0.2
0.1
SHORE PROFILE
ELWS
2
4
6
8
HORIZONTAL DISTANCE (m)

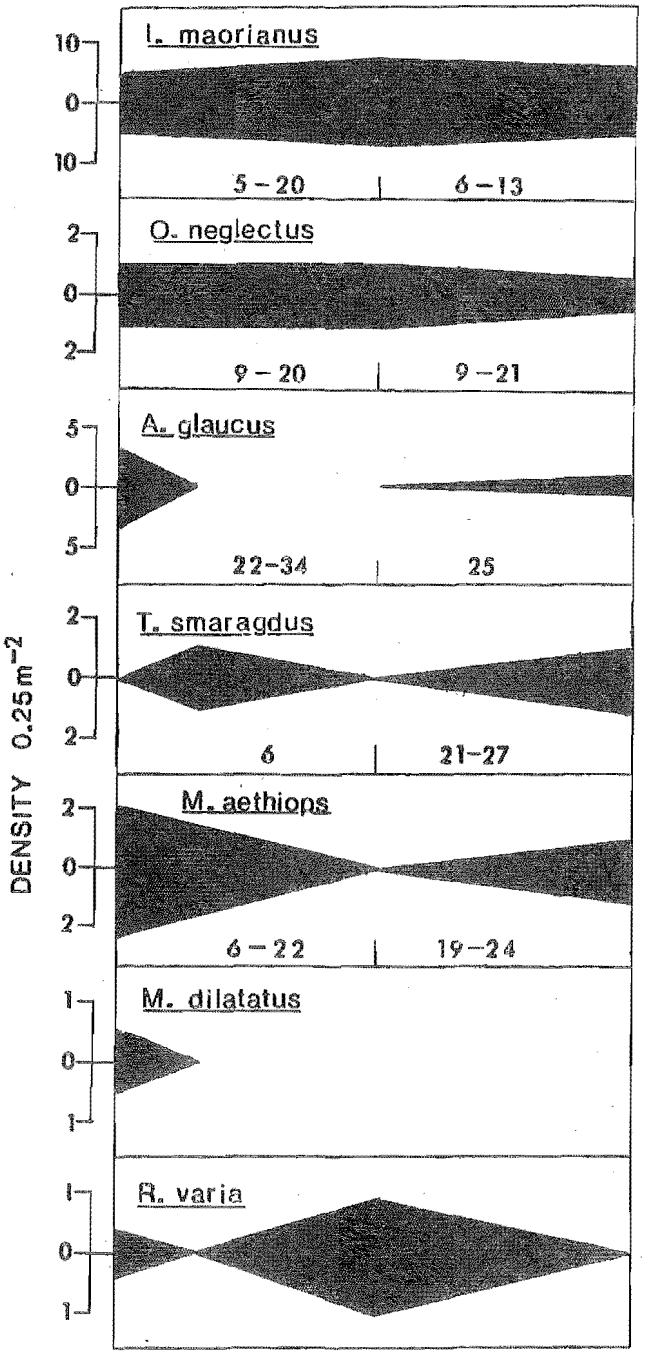
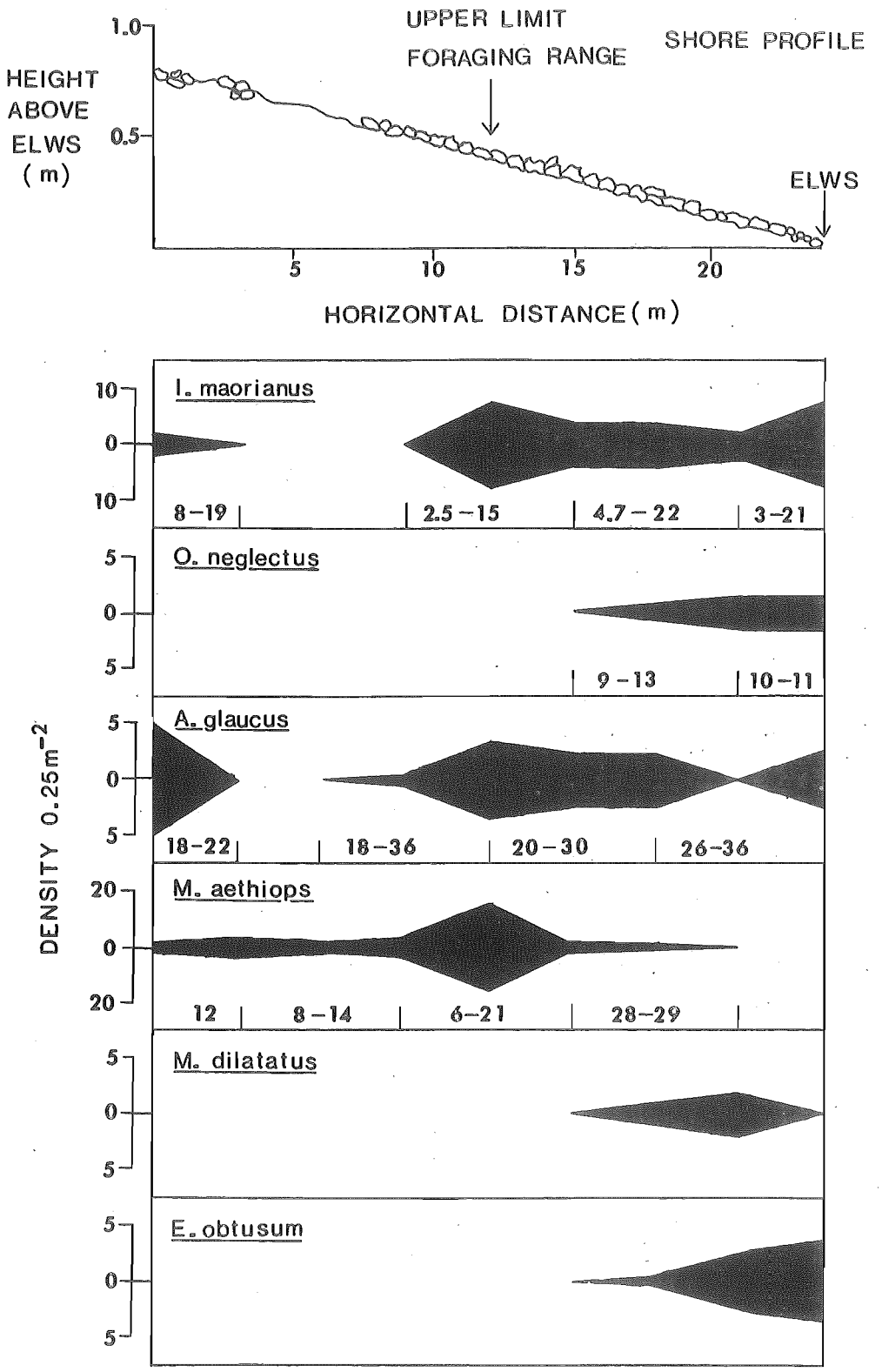

I. maorianus
10
0
10
5 – 20
6 – 13
O. neglectus
2
0
2
9 – 20
9 – 21
A. glaucus
5
0
5
22–34
25
T. smaragdus
2
0
2
6
21–27
M. aethiops
2
0
2
6 – 22
19–24
M. dilatatus
1
0
1
R. varia
1
0
1
DENSITY 0.25 m⁻²

FIGURE 7.18: Vertical distribution and mean density patterns of major prey species at site 4. (Figures at intervals in prey distribution patterns are prey size range at that stratum.)


UPPER LIMIT
FORAGING RANGE
SHORE PROFILE
HEIGHT ABOVE ELWS (m)
1.0
0.5
ELWS
5
10
15
20
HORIZONTAL DISTANCE (m)
DENSITY 0.25m⁻²
I. maorianus
10
0
10
8-19
2.5-15
4.7-22
3-21
O. neglectus
5
0
5
9-13
10-11
A. glaucus
5
0
5
18-22
18-36
20-30
26-36
M. aethiops
20
0
20
12
8-14
6-21
28-29
M. dilatatus
5
0
5
E. obtusum
5
0
5

seastar, these two species together with *I. maorianus* had a large degree of overlap with *A. scabra* as juveniles and adults. These data suggest that small *M. aethiops* had less overlap with the seastar than adults, and at all localities, small *M. aethiops* remained in sheltered positions at low tide, often on the undersides of rocks, whereas large specimens inhabited boulder tops. *R. varia*, *M. dilatatus* and *E. obtusum* were present in low densities at all sites. *R. varia* was most abundant at site 3, and this was reflected in its importance in the diet of seastars there. Similarly, dense aggregations of *T. smaragdus* at site 1 probably accounted for its importance as food at that site. *I. maorianus* was the dominant prey chiton at all localities. *A. glaucus* appeared slightly more frequently as food at site 4. It was here that *A. glaucus* had its densest population, and a high level of spatial overlap with *A. scabra*.

Clearly, dietary composition at any location depends, to some extent, on the degree of prey-predator spatial overlap. It follows then that the size-frequency characteristics of the overlapping portion of the potential prey species population influence the size composition of the diet.

Although there was no separation of juvenile and adult micro-habitat, the smaller size classes of *T. smaragdus* were discriminated against to the extent that not a single specimen of less than 21mm shell height appeared as a prey item throughout the study period ($e = -1$) (Fig. 7.19). There was no size-discriminant predation by seastars on *T. smaragdus* of between 21-34mm shell height ($x^2 = 20.27$, d.f. = 13, $p > 0.05$). *T. smaragdus* has no escape reaction from *A. scabra* (Chapter 6), and its heavy operculum apparently affords little protection from the seastar. Despite these factors and its predominance as a food item at site 1, only about 3.5% of available, large *T. smaragdus* were consumed per year (Chapter 4).

A similar size-discriminant pattern existed for predation on *R. varia* (Fig. 7.20). Again, preferential feeding on the largest members of the available population is a mechanism which ensures the best return per foraging effort and the factors causing the observed pattern may be identical with those in the *A. scabra - T. smaragdus* interaction. *R. varia* has an escape reaction, but does not achieve a refuge in size from predation. Even at its maximum size (shell height 7mm), the resultant mean predator/prey size ratio was high (8.9), and probably rendered the escape reaction ineffective or of low efficiency. Although no evidence exists to substantiate the suggestion, this may be a local phenomenon, peculiar to this prey/predator interaction, and the response may be effective against smaller predacious asteroids at other localities. In contrast with *T. smaragdus* and *R. varia*, small specimens of *M. aethiops* (up to 8mm shell height) were favoured prey ($e = 0.48$) (Fig. 7.21), as were individuals of 18-23mm shell height ($e = 0.24$). The mean size of seastars which preyed upon 3-8mm animals ($\bar{Rx}$ = 56.6mm, S.D. = 21, n = 26) was significantly different from those which preyed upon 18-23mm *M. aethiops* ($\bar{Rx}$ = 87.9mm, S.D. = 27, n = 10) (Mann-Whitney U test, U = 330, n = 36, $p < 0.01$). This explains, in part, why seastar size classes may have large degrees of dietary overlap in terms of prey species, but can simultaneously have little overlap in terms of prey size.

M. dilatatus of 5-6mm shell height were consumed preferentially ($e = 0.38$) (Fig. 7.22) by seastars of mean size $\bar{Rx}$ = 60.9 (S.D. = 16.8, n = 25), comparable to those which preyed upon 3-8mm *M. aethiops*. No significant linear relationship between prey size and predator size was found in the *A. scabra - M. dilatatus* interaction.

Size-discriminant predation patterns for *I. maorianus*, *O. neglectus* and *A. glaucus* were essentially alike (Figs 7.23, 7.24, 7.25). All three species were favoured at lengths of 11-19mm, and

I. maorianus to 23mm. At lengths of 23-27mm all three species were discriminated against. *O. neglectus* of 11-19mm were consumed by seastars of a mean size ($\bar{Rx}$ = 65.5, S.D. = 15.6, n = 14) significantly different (Mann-Whitney U test, U = 106, $p < 0.01$) from those which consumed 27-31mm specimens ($\bar{Rx}$ = 90.7, S.D. = 33.8, n = 4). Partitioning of prey amongst seastar size classes did not occur in *A. glaucus* for which the mean size of seastars preying upon 11-19mm and 27-39mm animals was not significantly different ($\bar{Rx}$ = 69.1mm and 77.5mm respectively, U = 67, n = 21, $p > 0.05$).

FIGURE 7.19: Size discriminant predation pattern for *T. smaragdus*. The upper size frequency distributions are significantly different ($x^2 = 53.8$, d.f. = 18, $p < 0.001$).

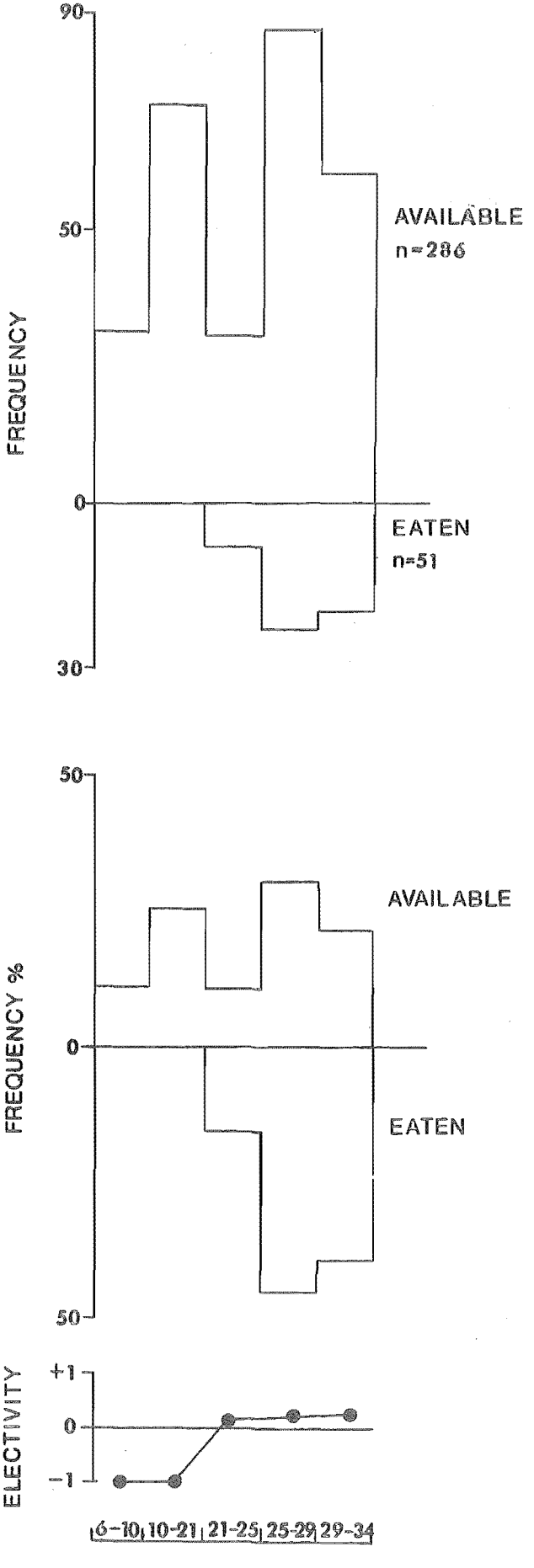

90
50
0
30
FREQUENCY
AVAILABLE
n=286
EATEN
n=51
50
0
50
FREQUENCY %
AVAILABLE
EATEN
+1
0
-1
ELECTIVITY
6-10
10-21
21-25
25-29
29-34
SIZE CLASS(mm)

FIGURE 7.20: Size discriminant predation pattern for *R. varia*. The upper size frequency distributions are significantly different (x^2 = 41.5, d.f. = 4, $p < 0.001$).

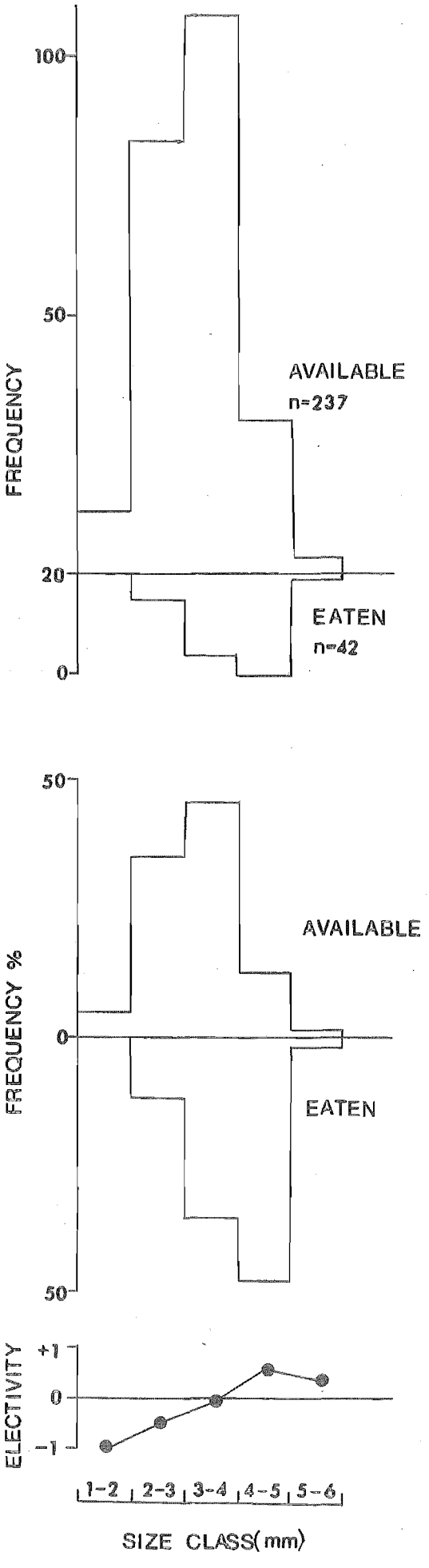
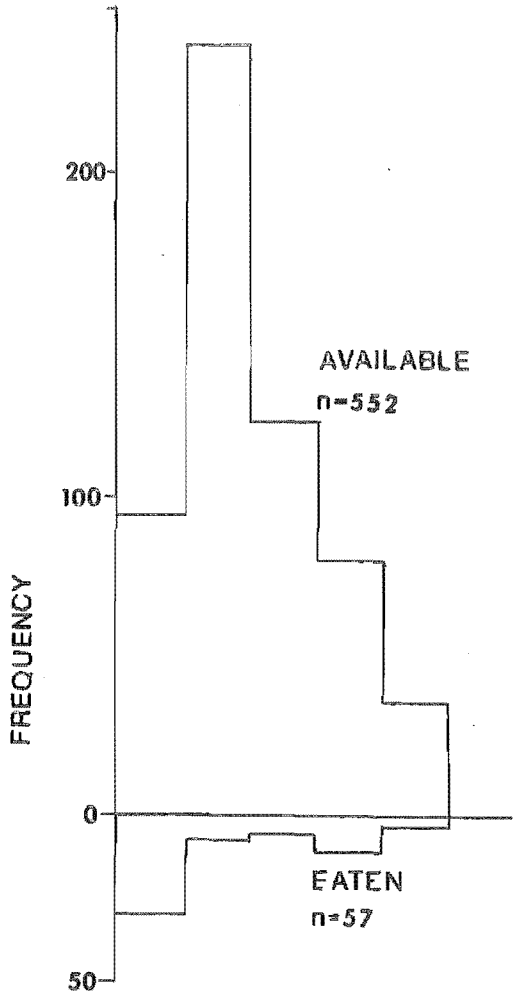

100
50
20
0
FREQUENCY
AVAILABLE
n=237
EATEN
n=42
50
0
50
FREQUENCY %
AVAILABLE
EATEN
+1
0
-1
ELECTIVITY
1-2
2-3
3-4
4-5
5-6
SIZE CLASS(mm)

FIGURE 7.21: Size discriminant predation pattern for *M. aethiops*. The upper size frequency distributions are significantly different ($x^2 = 65.0$, d.f. = 24, $p < 0.001$).


200
100
0
50
FREQUENCY
AVAILABLE
n=552
EATEN
n=57

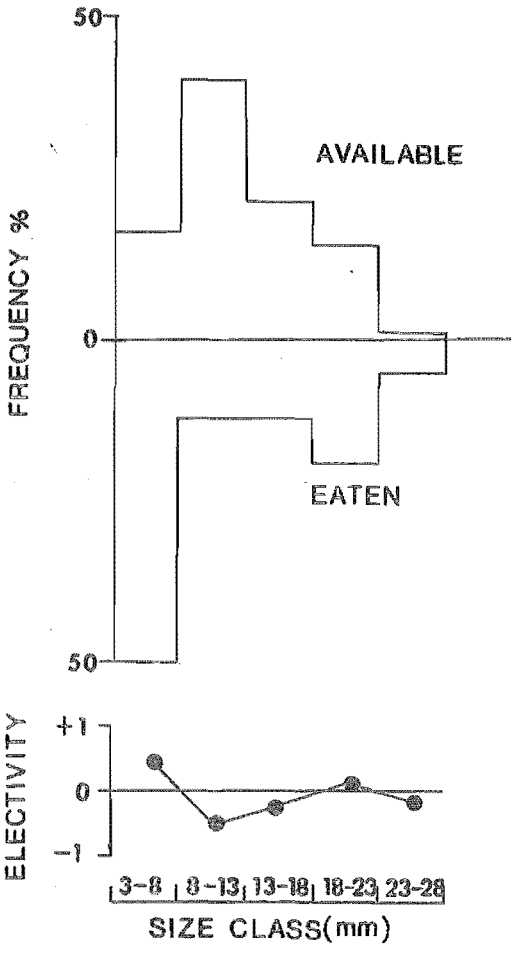
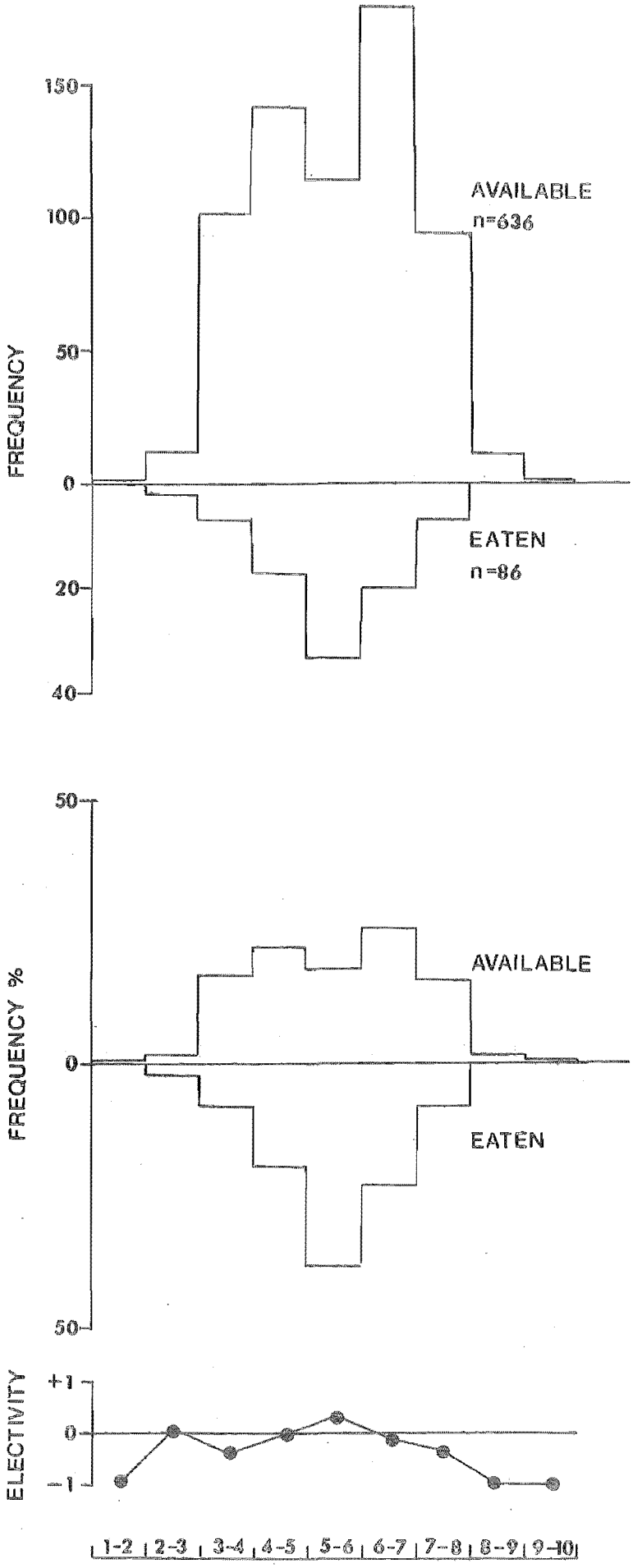

50
0
50
FREQUENCY %
AVAILABLE
EATEN
+1
0
-1
ELECTIVITY
3-8
8-13
13-18
18-23
23-28
SIZE CLASS(mm)

FIGURE 7.22: Size discriminant predation pattern for *M. dilatatus*. The upper size frequency distributions are significantly different ($x^2 = 33.6$, d.f. = 8, $p < 0.005$).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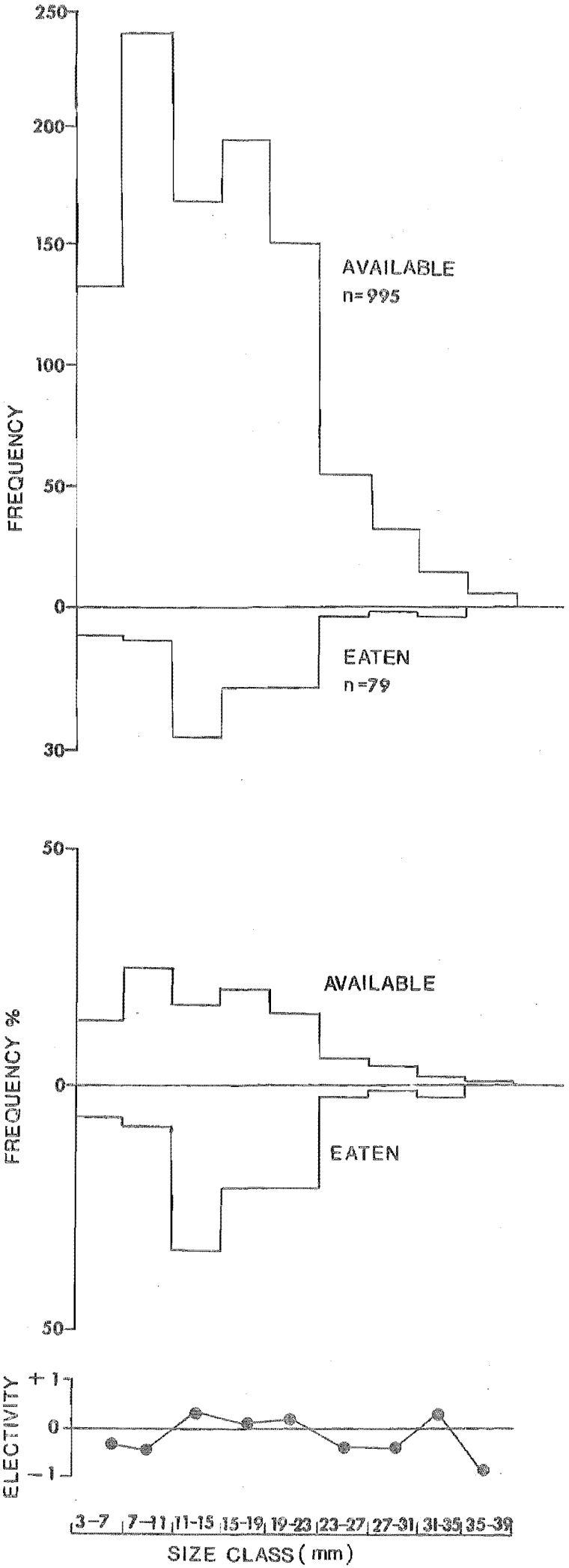
100
50
0
20
40
FREQUENCY
AVAILABLE
n=636
EATEN
n=86
50
0
50
FREQUENCY %
AVAILABLE
EATEN
ELECTIVITY
+1
0
-1
1-2
2-3
3-4
4-5
5-6
6-7
7-8
8-9
9-10
SIZE CLASS(mm)

FIGURE 7.23: Size discriminant predation pattern for *I. maorianus*. The upper size frequency distributions are significantly different (x^2 = 70.2, d.f. = 36, $p < 0.005$).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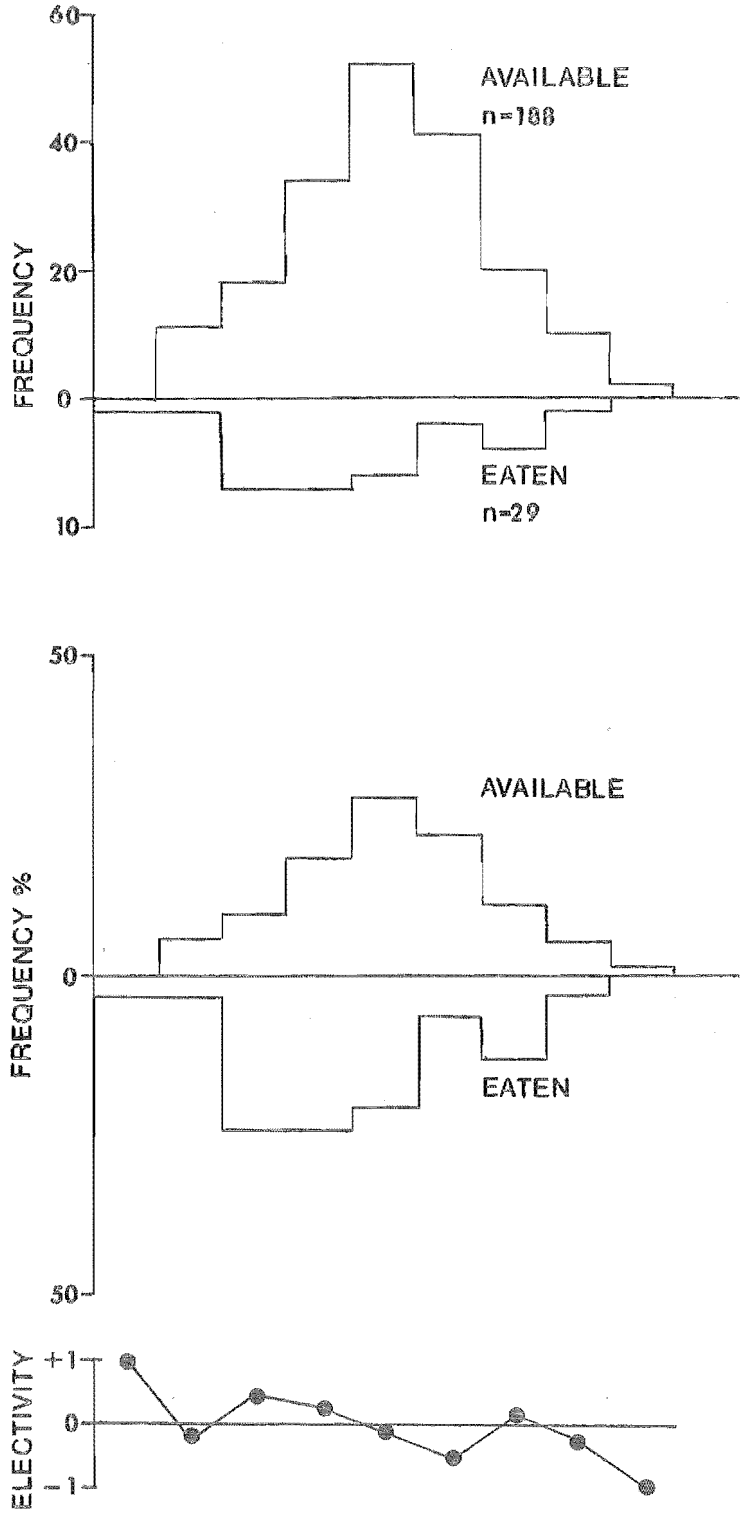
200
150
100
50
0
30
FREQUENCY
AVAILABLE
n=995
EATEN
n=79
50
0
50
FREQUENCY %
AVAILABLE
EATEN
+1
0
−1
ELECTIVITY
3–7
7–11
11–15
15–19
19–23
23–27
27–31
31–35
35–39
SIZE CLASS (mm)

FIGURE 7.24: Size discriminant predation pattern for *O. neglectus*. The upper size frequency distributions are significantly different ($x^2 = 57.9$, d.f. = 8, $p < 0.001$).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20
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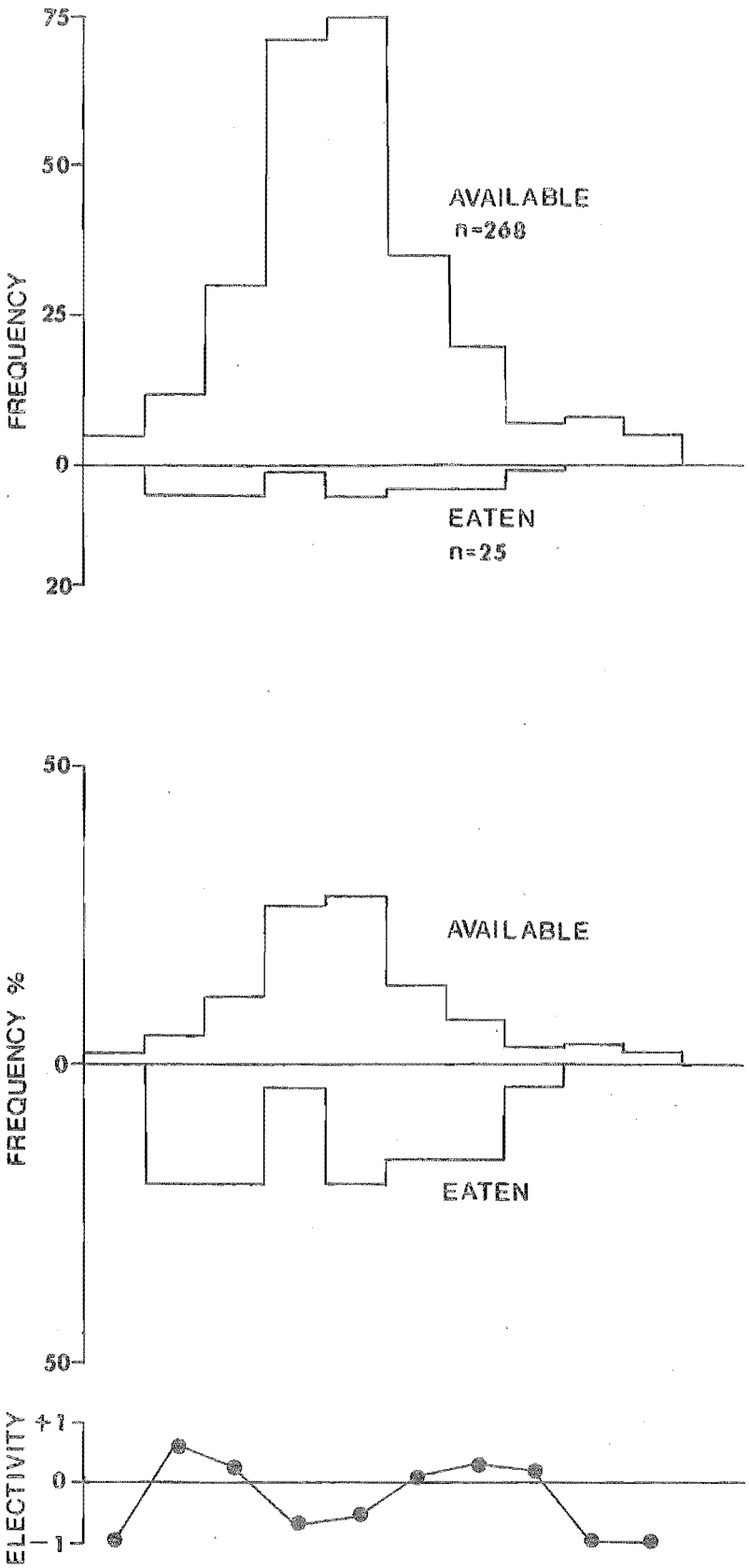
10
FREQUENCY
AVAILABLE
n=188
EATEN
n=29
50
0
50
FREQUENCY %
AVAILABLE
EATEN
+1
0
-1
ELECTIVITY
3-7
7-11
11-15
15-19
19-23
23-27
27-31
31-35
35-39
SIZE CLASS (mm)

FIGURE 7.25: Size discriminant predation pattern for *A. glaucus*. The upper size frequency distributions are significantly different ($x^2 = 55.7$, d.f. = 35, $p < 0.025$).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50
25
0
20
FREQUENCY
AVAILABLE
n=268
EATEN
n=25
50
0
50
FREQUENCY %
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EATEN
+1
0
−1
ELECTIVITY
7-11
11-15
15-19
19-23
23-27
27-31
31-35
35-39
39-43
43-47
SIZE CLASS (mm)

CHAPTER 8. DISCUSSION

INTRODUCTION

Most carnivorous asteroids are food generalists, although they will often preferentially consume particular species in laboratory trials, or in nature if a single, acceptable food is especially abundant (Mauzey *et al.*, 1968). The degree to which seastars have generalised or specialised diets is independent of substrate or depth (Mauzey *et al.*, 1968). In nature, long-term dietary composition is related directly to the regularity with which depleted food stocks are replenished (Menge, 1972b; Birkeland, 1974). A single, irregularly replenished food source cannot be preferentially consumed as specialisation on such a prey may deplete the stock to a level at which it becomes too sparse to support the predator population (Menge, 1972a). Complete monotony in asteroid diets appears to be rare. A notable exception is *Hippasteria spinosa*, a near obligate food specialist which preys upon the sea pen, *Ptilosarcus gurneyi* (Birkeland, 1974). Food specialists may be rare because they require plentiful numbers of single prey species, whereas feeding in food generalists is unaffected by any fluctuations in the population density of single prey species. Further, small prey generalists survive better than small specialists because the former can find a greater range of possible prey within their limited cruising range (Birkeland, 1974). Furthermore, a specialised predator's reproduction, recruitment, dispersion, and growth are likely to be affected by the abundance of its prey source. Compared with food generalism, this is a dangerous life history tactic, as physical or biotic factors which may not affect the predator directly, may indirectly influence prey survival and recruitment and thereby have

a deleterious effect on the predator population.

Seastars with generalised diets can adjust their body size, through growth, to suit local conditions, and reproduction can be partly independent of prey community characteristics (Paine, 1976). Thus, *Pisaster ochraceous* is a food generalist (Feder, 1959), has a preference for mussels (Landenberger, 1968), is widely distributed from Alaska to Mexico (Feder, 1959; Hopkins and Crozier, 1966), and survives and reproduces in areas not containing its preferred prey (Mauzey, 1966). The occurrence of acceptable food is a prime determinant for the presence of seastars (Galtsoff and Loosanoff, 1939; Hancock, 1958; Ursin, 1960; B. Rasmussen, 1965), and asteroid population densities may be regulated by prey densities (Larsson, 1968). A long-term survey by Loosanoff (1964), however, demonstrated that recruitment of *Asterias forbesi* over a 25 year period could not be correlated with settling of oysters, its preferred prey. Growth and reproductive output in asteroids is related directly to the amount of available food (Smith, 1940; Needler, 1941; Vevers, 1949; Pearse, 1965; Feder, 1970; Birkeland, 1974).

Predictions regarding a predator's optimal use of food resources have been made by a number of workers. MacArthur and Pianka (1966) proposed that an activity (in this case, food generalisation or specialisation) should be promoted as long as there is a reduction in search time. If further development of the activity results in increased search time, then no subsequent development should take place. The risk in adopting food specialism is that a preferred prey species, when exploited, becomes less densely distributed to the extent that specialisation is energetically impracticable. Christensen (1970) regarded asteroids as hunters and MacArthur and Pianka (1966), Emlen (1968) and Pulliam (1974) suggested that pursuers should restrict the

range of prey taken when food is abundant, and should become less selective when food is scarce, as predators can locate and catch clumped prey most easily. Food generalism or specialism (within the constraints of a fixed hunting technique) are the result of both food density and prey mobility (MacArthur and Pianka, 1966). Emlen (1966) agreed with Elton (1947) in the view that animals may feed most frequently on abundant food types, to the exclusion of richer and more efficiently exploited species. Mobile prey, or prey with escape reactions, require relatively long pursuits, and ideally food specialists should consume sessile species. Indeed, *H. spinosa* eats *P. gurneyi*, which although capable of contracting into sandy substrates, displays little lateral movement (Birkeland, 1974). A predator's optimal diet is the series of successive prey choices which maximises the rate of calorific intake, or alternatively minimises the time required to find a food ration (Pulliam, 1974). The extent to which potential food is neglected can indicate if food availability limits predator numbers (Emlen, 1966).

Dietary composition in *A. scabra*

At Kaikoura, *A. scabra* is a food generalist at all study sites throughout the year; few prey species were eaten often, but many were eaten occasionally. Predator foraging strategy and selectivity did not change seasonally and were thus independent of fluctuating physical factors and small variations in prey community composition (Chapter 4). In contrast, *P. ochraceous* of the north-western Pacific eats only chitons in winter (Mauzey, 1966). It is suggested that *A. scabra* at Kaikoura is a food generalist because no single, acceptable prey species is abundant or replenished enough to permit specialisation. The relative dearth of potential sessile prey within the foraging range of *A. scabra* at Kaikoura might also be a determinant in promoting food generalism. At Kaikoura, *A. scabra* ate as many as 52 prey species at

any one site (Fig. 4.5). This occurred in spite of high densities of major prey items (Table 4.9). The predator did not therefore restrict the range of prey taken in spite of prey being densely distributed (cf. MacArthur and Pianka, 1966; Emlen, 1968; Pulliam, 1974). At site 4, *A. glaucus* was eaten more frequently than *I. maorianus*. The latter chiton has no escape reaction, and yields the same biomass, adheres less strongly, and is more abundant than the former chiton. Emlen's (1966) view that prey abundance is the prime determinant of dietary composition is thus not supported by this result. Although the diet at each site, of necessity, reflected the differing composition of the prey community, it was independent of the absolute abundance of potential prey species (Table 4.9).

Numbers of *A. scabra* do not appear to be regulated by food availability as this species neglected some potential food sources, including the abundant trochid, *Diloma arida* and small *T. smaragdus*. Major prey species such as *I. maorianus*, *M. aethiops* and large *T. smaragdus* were also lightly exploited. Despite differing densities of major prey at each site, the numbers consumed per m^2 per year were similar for all sites, and only *T. smaragdus* at site 1 and *M. dilatatus* at site 2 suffered a removal rate in excess of 1 per m^2 per year.

The extremely generalised nature of the diet of *A. scabra* overcomes the potentially limiting effects of food availability on predator numbers. Also, intertidal populations of *A. scabra* are not dense (6-7 / $100m^2$, Table 4.3) especially considering Menge (1972a) believed *P. ochraceous* to be scarce at densities of 13/$100m^2$. Food generalisation reflects the balance between the abundance and replenishment rate of acceptable food, and may be viewed in the present case as opportunistic feeding on relatively abundant chitons and trochids which occurred in clumps and formed almost 36% of the prey of *A. scabra*. The consumption of abundant prey such as *I. maorianus*,

M. aethiops and large *T. smaragdus* by *A. scabra* minimises the time required to find food, and this implies that *A. scabra* is indeed feeding in an optimal manner (Pulliam, 1974).

On the basis of a few observations in Otago Harbour, Crump (1969) concluded that *A. scabra* was an exclusively nocturnal feeder. This assessment is contrary to the observed tidal rhythm of feeding typical of intertidal seastars in general, and does not agree with my daytime and nocturnal observations on intertidal and subtidal *A. scabra*. The tidal rhythm of feeding in intertidal *A. scabra* is the result of two influences. *A. scabra* can forage only when submerged, and must cease feeding at low tide and return to rock undersides to eliminate the risk of osmotic stress from rainfall or desiccation. Animals which remain on exposed rock upper surfaces in summer can be subjected to temperatures of 45°C and could be frozen in winter (Ottaway, 1977). It is unlikely that exposed seastars would suffer from predation. *A. scabra* apparently has no predators; shore birds showed no interest in whole or dismembered specimens, and there is only one record of predation by fish (Godfriaux, 1969).

I conclude that the annual feeding cycle is due to locomotion being inhibited by low winter temperatures. Intertidal *A. scabra* are predominantly immature, and reproductive activity cannot be involved. Storms occur throughout the year, and do not in themselves interrupt feeding. Prey abundance does not vary markedly during the year. The disruption of the annual cycle during November 1976 and January 1977 was due to inhibition of feeding in seastars at sites 2 and 3, probably caused by extensive localised inputs of freshwater from the Wairere Stream.

Selective feeding

A predator feeding according to the dictates of the optimal diet

should show no partial preferences (Pulliam, 1974). In point of fact, partial preferences which lead to reduced search time or increased calorific uptake should persist within the behavioural framework of the predator. Emlen (1966, 1968) considered that predators should be more selective in their choice of foods when satiated or when food is abundant, and more indiscriminate when starved or when food is scarce. In my experiments (Chapter 5), starved *A. scabra* were not only capable of discriminating between different food types, but also preferentially consumed *I. maorianus* (Table 5.3). Christensen (1970) and Fenchel (1965) discovered that both *Astropecten irregularis* and *Luidia ciliaris*, in the absence of preferred food, either fed less or began to starve. Emlen's view that starvation leads to indiscriminate feeding may be incorrect. Prey selection by *A. scabra* in laboratory conditions might have been influenced by reduced environmental stress, such as lack of fluctuations in temperature, increased submergence and feeding times, lack of water turbulence, and artificial confinement of prey organisms. Furthermore, only a limited prey spectrum of three species was presented in each experiment, and the manipulated prey densities were higher than those which prevail normally in nature. This high, relative abundance of prey may have overridden any tendency toward indiscriminate feeding caused by starvation. Although predator food preferences are weaker when many alternatives are present, this in itself probably does not have any long-term effect on selectivity in nature (Landenberger, 1968). Food preferences determined experimentally in this study should be considered only with reference to the *A. scabra* population at Kaikoura. Such behavioural traits may develop soon after metamorphosis and might only reflect the particular prey assemblage with which the seastar is associated. These experiments revealed a "generality of preferences" in that chitons and trochids appeared to be more-or-less equally attractive as food. Further, in both my experiments, the

preferred species constituted 63% of all prey consumed and were not eaten to the total exclusion of other species. Food generalism (partial specialisation) appeared to have an inherent limit. A generality of food preferences has high adaptive value because a seastar can still feed during a dearth of its preferred prey species, and growth and reproduction can continue. Generalised preferences, or preferences which develop according to the character of the assemblage with which the asteroid is associated, partially relieve the potentially limiting effects of food, enlarge the number of sites acceptable to the seastar, enhance dispersal of the species, and allow the seastar to utilise dense patches of food where and when they occur. Animals found with the stomach everted on to a variety of substrata were probably utilising detritus (Mauzey, 1966). The ability to consume this material is a further expression of food generalisation, and also confers the above advantages on the species.

Menge (1974) suggested that a predator species may maintain a preference "polymorphism" in the population so that feeding is generalised, but individuals are specialised. Dietary diversity was related directly to the number of seastars feeding (Fig. 4.8) and at no time was one prey species eaten exclusively by the whole seastar population. Of all prey species, only *T. smaragdus* at site 1 occurred in every collection (Table 4.4). The existence of specialised individuals within the predator population would require that some prey species occur in every collection at each site. This did not occur, and it is therefore improbable, with the exception of the largest specimens, that individual *A. scabra* are specialised.

Food preferences isolated in the laboratory relate to a set of prey sizes. Prey attractiveness is linked with species, and secondarily to size (Christensen, 1970). Therefore, in the present study, *M. dilatatus* could have been strongly discriminated against not because

of any inherent distasteful character, but because alternative prey were present. Selection of prey according to species is the result of ease of capture, prey/predator size ratio, escape reactions, pursuit and handling time, and calorific yield (Menge, 1972b). The last influence must have developed over evolutionary time as a seastar presumably cannot "taste" calorific yield prior to digestion. Natural selection should have advantaged those seastars which preferentially consumed species of high calorific yield. Significantly, Menge (1972a) reported that energy-low species were numerically dominant in the summer diet of *Leptasterias hexactis*, a time when feeding in this species proceeds at its maximum rate. Prey calorific yield may therefore be secondary to availability in the determination of seastar diets.

Although prey discriminant feeding was evident under laboratory conditions, it is difficult to demonstrate in the field. However, if the diet is a statistically non-random representation of spatially available species, and if potential prey community diversity exceeds dietary diversity, then selective feeding must have been undertaken (Landenberger, 1968). These criteria are met by *A. scabra* in the Kaikoura region, as dietary proportions, prey removal rates and predator preferences are independent of prey densities (Tables 4.9, 5.3).

Paine (1969b) was of the opinion that as long as a prey did not reach preferred status with its principal predator, then co-existence was selected for. Indeed, in some prey populations, predation can increase reproductive potential by reducing crowding and relieving competition for limited resources. However, in the *A. scabra - I. maorianus* interaction, the latter is the preferred prey, and in the absence of predation on the seastar, overexploitation (the point where search time exceeds food gain), might be possible (Paine,

1969b; Dayton *et al.*, 1977). If the preferred prey of a food generalist is overexploited, feeding will continue on more or less equally attractive food (Christensen, 1970), while the preferred prey recovers from predation pressure. Further, the partial preferences are such that trochids are equally as attractive as chitons, and predation on a secondary choice prey may indirectly have a positive effect on the recruitment of the preferred form, if resources are limiting and competition between prey is strong (Dayton, 1971). Prey species can avoid overexploitation by high growth rates, early maturity, high reproductive rates, and through possession of spatial and size refuges (Christensen, 1970).

The perceptive abilities of *A. scabra* which enable it to discriminate between prey species are probably chemotactic. This conclusion is supported by the following evidence. The existence of unidirectional currents in exposed boulder habitats is likely to be very rare and of a transient nature. The ability to discern the presence of prey at a distant point along a physical gradient would therefore be of little use to a seastar. The slow, but partially effective escape reactions of *O. neglectus* and *A. glaucus* suggest that chemotactic clues are most important because when responding, these chitons cannot outrun seastars, and this infers that once contact between the two has been lost, the predator has no way of tracking the prey (Menge, 1974). Asteroid chemoreceptors are located on distal tube feet and sensory tentacles, and should be well developed especially since photoreceptors are poorly represented (Valentincic, 1973). Christensen (1970) noted that short distance perception was of decisive important in prey location by *Astropecten irregularis* and that long distance perception was of little use. Prey were assessed during foraging and not after capture, i.e., the asteroid was an active hunter. Dayton *et al.* (1977) viewed seastars as searchers, which suggests that

contact chemoreception was of primary importance. Loosanoff and Shipley (1947) demonstrated that *Asterias forbesi* found prey by contact. *A. forbesi* and *A. vulgaris*, although capable of detecting prey at a distance, in unidirectional currents, did not behave entirely predictably (Whittle and Blumer, 1970; Zafiriou, 1972; Zafiriou *et al.*, 1972). In identical conditions, *A. rubens* had seasonally variable responses (Castilla and Crisp, 1970; Castilla, 1972a, 1972b). Blake (1960) and Kohn (1961) noted that species-specific metabolic products liberated by potential prey were distinguished by carnivorous gastropods and mediated the predator's choice of an individual within a group of prey.

Prey escape reactions

The results of escape response studies have interesting implications in the consideration of dietary composition. The persistence of an escape reaction in the locomotory repertoire of a potential prey species implies that organisms endowed with such ability have an increased chance of survival in the face of predation. However, Olsen (1955) found that predation by *Coscinasterias calamaria*, over a 4 year period, caused 75-80% mortality in the Tasmanian scallop, *Notovola meridonalis*, which reacts to contact with the asteroid by "flipping" off the seabed and swimming a short distance (D.C. Wolfe, pers. comm.).

Escape responses in the abalone *Haliotis iris*, *H. australis* and *H. virginea* are very effective in reducing predation. Dense aggregations of the first species persist from year to year with little evidence of seastar predation. The retention of vigorous escape reactions by these species casts further doubt on the views of Feder (1959), Cox (1962) and Montgomery (1967) (Chapter 6) that seastars are not important potential predators of abalone. The effectiveness of the

escape response in *Cellana radians*, in nature, is difficult to assess. The low-shore form of this species is distributed very sparsely and patchily. The response was consistently effective in the laboratory. The gradation of response magnitude in the three *Cellana* species tested corresponds with the degree of vertical spatial overlap each species has with *A. scabra*. Low-shore *C. radians* tested in the experiments have the greatest amount of overlap with the predator and the most marked escape reaction. The vertical distribution of *C. ornata* and *C. denticulata* is determined by their intolerance of constant immersion (R. Rasmussen, 1965). This physiologically controlled distribution means that these two species reside ordinarily above the seastar's foraging range and are not liable to predation. The possession of an escape reaction therefore is redundant and the lesser vigour of their responses is probably a preliminary stage in the complete loss of the response. This is analogous with the situation described by Feder (1963) in which *Acmaea* species showed a graded series of defensive reactions commensurate with their overlap with *Pisaster ochraceus*.

The low level of predation on the fissurellid, *Scutus breviculus*, was due either to low desirability or to its escape reaction. Escape reactions in trochids appeared to be very effective in reducing mortality through predation. Partly because of the escape responses, large *M. aethiops* are available only to large seastars, and discrimination against large *M. dilatatus* presumably reflects the point at which pursuit effort is not repayed.

There is significant adaptive value in the sophisticated ability displayed by abalone and *A. glaucus* to distinguish foraging, from non-foraging seastars. To react to a close, quiescent seastar during low tide can expose the mollusc to desiccation, freezing, rainfall, or predation by shore birds. In subtidal situations, described by Dayton *et al.* (1977), in which potential molluscan prey react only to actively

foraging seastars by expansion of the mantle margin, and subsequent release of their grip on the substratum causes them to be washed away. In this case, the molluscs can be exposed to other predators such as fish, or may be transported to unsuitable habitats such as sand, to which they may be intolerant.

The absence of escape responses in prey species which overlap spatially with *A. scabra* is puzzling. These species, which included *T. smaragdus, I. maorianus, Buccinulum vitatum, Siphonaria zelandica* and *Prototháca crassicosta*, may have some other defensive character. Apart from *I. maorianus* and *T. smaragdus,* non-responsive organisms were generally minor food sources and were distributed sparsely within the asteroid's foraging range. These may have escape in structure, "bad" taste, or rapid growth into size refuges. Historically, predation pressure on these species may never have been of sufficient magnitude to differentially favour individuals with escape reactions, or such a response may never have developed. The absence of a response in *I. maorianus*, which is closely related to *O. neglectus* and *A. glaucus,* can be ascribed to one of two mechanisms. The response, possibly of great antiquity, has been lost because an annual starfish predation rate of about 5% has not been sufficient to sustain retention of the escape response. Alternatively, escape responses may have evolved independently in different species and might be similar in closely related species, as an escape reaction is a modification of normal movement which, in chitons, is of limited scope.

Accounts of molluscan habitatuation to, or fatigue from, the constant presence of predacious asteroids unfortunately do not distinguish whether the seastars were actively foraging. Molluscan habituation to the constant presence of predacious asteroids may have some adaptive value. Habituation can occur only if the potential prey is not eaten, or if the execution of the escape reaction has not

separated the predator from the prey. In either case, that the prey has not been eaten after the passage of some time might indicate that an attack by the predator is not imminent, and the potential prey need not expose itself to the risks outlined above.

Prey which suffer least, in per cent annual removal rates (*I. maorianus* and *T. smaragdus*) are species without escape reactions, and which are preferred by all or part of the seastar population. Escape responses might be unnecessary because of the low level of exploitation and the predator's preference for these species may have arisen through the lack of response (Phillips, 1977).

Biotic factors and dietary composition

I suggested earlier that *A. scabra* was feeding in an optimal manner, and Pulliam (1974) considered that a predator feeding so as to maximise its calorific intake should take a specific prey item on every ecnounter with it, or not take that item at all. The prey community at Kaikoura is probably "fine grained" (i.e. potential prey were located in proportion to their abundance) (MacArthur and Pianka, 1966), but prey- and size-discriminant feeding occurred not only because seastars probably were obtaining the best return for foraging effort, but also because they have to maximise their food intake during the limited feeding periods imposed by a tidal regime. Only large *T. smaragdus* and *R. varia* (for example) were eaten, and small specimens were wholly neglected. This is analogous to the situation described by Paine (1969b) in which the brunt of predation on *Tegula funebralis* by *P. ochraceous* was borne entirely by the larger, co-occurring individuals. These results support Pulliam's (1974) prediction. The observed size-discriminant predation on *T. smaragdus* may be generated by several factors. Small *T. smaragdus* may not trigger the seastar's chemosensory/ tactile system. This seems improbable in view of the small size of

other prey species, and because small *T. smaragdus* were eaten by starved *A. scabra* in laboratory aquaria. Small *T. smaragdus* may be less preferred than other co-occurring, more abundant prey such as *I. maorianus* (Fig. 7.17), and the former species may thus be "passed over" in favour of other species. Large *T. smaragdus* were eaten by large seastars ($\bar{Rx}$ = 132.9mm, S.D. = 49.6, n = 49) and although small *T. smaragdus* may represent an adequate return per foraging effort for small seastars, the latter may not be able to overcome the sealing effect of the operculum at the prevailing seastar/prey size ratio. Further, the presumably endogenous criteria upon which prey preferences are based may change with increasing seastar size, and could be such that small *T. smaragdus* are actively discriminated against by small *A. scabra*. These data indicate that intertidal *T. smaragdus* have no refuge from predation in large size. On the contrary, they grow into a preferred size category, and are safe from predation by *A. scabra* when small. (The largest *T. smaragdus* of up to 60mm shell height, and which are entirely sublittoral in occurrence (R. Rasmussen, 1965) may represent specimens which have attained a size refuge from predation.)

Size-discriminant predation on *M. aethiops* is the result of the following parameters. First, small *M. aethiops* (<8mm) are photophobic and reside beneath rocks during low tide. With the return of the tide and the commencement of foraging by *A. scabra*, which itself remains under rocks at this time, these smaller trochids are likely to be the first to be contacted and consumed i.e. less foraging is required to contact these specimens. Second, *M. aethiops* has a vigorous escape reaction (Chapter 6), and the prey size/predator size ratio (Fig. 7.13) is structured partially by the escape reaction, such that large *M. aethiops* are available only to large seastars. Third, large *M. aethiops* (>8mm) not only occupy boulder tops, which makes them relatively less available, but range higher upshore than small

individuals (R. Rasmussen, 1965), which further enhances this effect. Rather than active selection of small *M. aethiops* by *A. scabra*, the observed pattern of size-discriminant predation is the result of the greater availability of small specimens.

The generalised patterns of spatial overlap (Figs 7.16, 7.17, 7.18) between the two species are misleading, as *M. aethiops* therefore has partial refuges from predation in terms of both space and size. At its largest size (shell height ≃28mm), *M. aethiops* would be available, in the catchable sense, only to seastars in excess of R = 164mm (Fig. 7.13), and they were rare in the intertidal zone (Chapter 2). Seastars of $R\bar{x} = 56.6$mm are able to catch *M. aethiops* of up to 8.3mm and the apparent discrimination against specimens of 8-18mm is probably due to the effect of their escape response making them relatively less available to smaller seastars, and in their representing an inadequate return per foraging effort for larger seastars. *M. aethiops* of 3-8mm shell height represent the "recruit class" and are not present throughout the year. At times of their absence, and because of the relative unavailability of 8-18mm animals, predation on intermediate sized *M. dilatatus* (another trochid) occurs (Fig. 7.3). *M. dilatatus* of 6-10mm shell height may be discriminated against in favour of 3-8mm *M. aethiops*, a preferred species (Chapter 5). Further, *M. aethiops* and all three major chiton species are preferred to *M. dilatatus*, co-occur spatially, and are in some cases more abundant (Figs 7.16, 7.17, 7.18). Strangely, prevailing prey densities (Table 4.9) dictated that a seastar moving at random was more likely to contact *M. aethiops* than *M. dilatatus*, so the dominant numerical role of *M. dilatatus* in the diet of *A. scabra* at sites 2 and 3 appears to depend on another undetermined parameter. Feeding on intermediate sized *M. dilatatus* could be the result of flexible predator preferences. If the predator, after some time, has been unable to secure its preferred prey, it may become less selective,

and so eats food of comparatively lower desirability (Menge, 1974).

Kohn and Nybakken (1975), in a study of feeding in a number of tropical intertidal *Conus* species (Gastropoda), discovered that food specialists fed more frequently than generalists, but both had similar prey weight intake rates as generalists ate large meals often enough to eliminate the difference. Although the low proportions of prey removed suggested that food was plentiful, they proposed that the preferential consumption of large prey items indicated that only a small proportion of the prey community was large enough to repay foraging effort and that prey may still be in short supply. Thus, similar limitations might cause the preferential consumption of the largest *R. varia* and *T. smaragdus* by *A. scabra*.

The five dietary shifts (Fig. 7.2), and increases in prey size with increased seastar size (Fig. 7.6) occurred because larger seastars need more food per unit time for self maintenance. Prey-selection criteria may change with predator size. Selection of large prey by large *A. scabra* may be permitted as increased predator diameter means a larger area is sampled per foraging period, which in a "fine grained" environment leads to more prey being sampled and discriminatory ability is enhanced by increased prey availability (Emlen, 1966, 1968). The prey- and size-discriminant feeding undertaken by *A. scabra* indicated that the seastar was not, as suggested earlier, feeding opportunistically, but sampled and evaluated a range of prey before selecting a food item; the latter might be compared to one recently digested. Identical constraints mould the diet of the predacious rocky intertidal snail *Acanthina punctulata* (Menge, 1974).

Most probably, *A. glaucus* and *O. neglectus* appeared later than *I. maorianus* in the diet of *A. scabra* (Fig. 7.4) as the seastar must be of a certain minimum size before the effects of the former two species' escape responses can be overcome. In addition, the force with which

these chitons adhere to the substrate varies according to species (pers. obs.). *A. glaucus* grips more firmly than *O. neglectus* which, in turn, is more firmly affixed to its substrate than *I. maorianus*. As the seastar prized chitons from rocks (Chapter 4), this phenomenon is likely to affect diet. The dietary shift, at R = 100-110mm to a diet dominated by *M. aethiops* and *T. smaragdus* is likely to be the result of two factors. First, the vigorous escape reaction of *M. aethiops* can be overcome only by large starfish, and second, large *M. aethiops* contain more consumable biomass than chitons of comparable size. The final dietary shift, by the largest seastars, to a diet consisting solely of *T. smaragdus* is clearly a mechanism which maximises the amount of food consumed per meal.

It is clear that large size does not necessarily confer immunity from predation on a potential prey species. The apparent dimensions at which prey species achieve a size refuge from predation may be the result of changed feeding behaviour or food preferences on the part of the predator. The size refuge, therefore, may not be achieved solely by growth of the prey. Size refuge and attractiveness limits may represent boundaries at which the predator does not, rather than cannot, eat the prey.

The absolute density of a prey species is no guide to its actual availability. Its mode of dispersion, degree of spatial overlap, and separation of microhabitat between size classes, all influence actual availability. So in gross terms, an individual prey item may apparently be available, but in actual terms, as with large *M. aethiops*, be unavailable as it occupies a spatial refuge within the habitat. Qualitative changes in dietary composition occur because with increasing size, the seastar is able to catch a broader spectrum of prey items and chooses those of best biomass yield i.e., food preferences do appear to change with predator size.

The three major chiton prey species were discriminated against at lengths of 23-27mm. Indeed, at these longest linear dimensions all species are available to seastars of R>100mm which, theoretically, would derive more benefit from the 0.3g of consumable biomass yielded by *M. aethiops* of similar linear dimensions than the 0.15g derived from chitons (Figs 7.9, 7.10). Mean sized seastars preying upon 11-19mm *I. maorianus* ($R\bar{x}$ = 67.2mm, S.D. = 24.3, n = 51), *O. neglectus* ($R\bar{x}$ = 65.5, S.D. = 15.6, n = 14) and *A. glaucus* ($R\bar{x}$ = 69.1, S.D. = 18.7, n = 10) would be able to catch *M. aethiops* of up to 10.3mm shell height. Consumable biomass yielded by 11-19mm chitons is about the same as that of 10.3mm *M. aethiops*, however, the latter, in view of its more vigorous escape behaviour, would be more difficult to pursue and catch. The preferential consumption of 11-19mm chitons therefore, in energetic terms, is likely to be more economical. It is not until chitons reach lengths of 30-40mm that they provide a consumable biomass yield similar to that of *M. aethiops* of the same longest linear dimension. *I. maorianus* is discriminated against at lengths in excess of 35mm, *O. neglectus* at 31mm, and *A. glaucus* at 39mm, but seastars of the size at which these chitons become available (Fig. 7.15) have already switched to *M. aethiops* and *T. smaragdus*, and the latter in particular yields far higher quantities of consumable biomass.

A foraging seastar can adopt one of three strategies. First, it can consume every prey item it encounters. Second, it can neglect smaller members of a prey community and pursue only larger individuals, and third, the latter can be discriminated against in favour of small prey items. The size-selective predation patterns determined for feeding *A. scabra* revealed that the first option was not taken up, and that the pattern generated depended on the prey species. Undirected wandering and pursuit of prey which may have vigorous escape reactions, low biomass yield, or are too large to be caught is energetically

wasteful and natural selection will have favoured those seastars which preferentially consumed available prey of adequate yield. Hard to catch species are the least available (Menge, 1972b). Doi (1976) considered that a seastar selecting smaller members of a prey community would obtain maximum food during limited feeding periods as large items require more handling time. However, only large *T. smaragdus* were eaten by *A. scabra*. This apparent contradiction is compensated for by the relatively high biomass derived from the consumption of this prey. Further, the presence of long-lived adult size classes of *T. smaragdus* (Walsby, 1977) is more predictable than that of recruits, and the occasional failure of recruitment will have little immediate effect on feeding by the seastar. The reproductive fraction of the *M. aethiops* population was subjected to less predation pressure by seastars, which in turn, in the absence of other predators, increases the likelihood that recruitment will occur in a temporally predictable manner.

These two predation strategies are mechanisms by which acceptable food sources are exploited in such a way that food supplies are assured in time. Similarly, the largest, and presumably most reproductively potent *I. maorianus, O. neglectus* and *A. glaucus* are immune from predation by *A. scabra* and this may also aid successful, predictable recruitment. Factors influencing predation on chitons relate not only to their desirability compared to other species, but also to their relative net biomass yield. In the interactions studied, the handling time, mode of prey dispersion, flesh weight-shell length characteristics, and time prey is exposed to the predator were the same for *I. maorianus, O. neglectus* and *A. glaucus*. *I. maorianus* appeared most frequently in the whole diet because it is most abundant, has no escape reaction, and generally is smaller than individuals of the other two species. Indeed, the seastar's preference for this species (Chapter 5) may be a function of these factors. In the field, *A. scabra* preferentially

consumed *I. maorianus* of slightly less than modal size (Fig. 7.23) such that consumed individuals generally were further from their species' size refuge limit than were chiton prey of the other two species. In this respect they matched the criterion erected by Doi (1976) as the optimal exploitable portion of a mixed prey population. *I. maorianus*, although patchily distributed, was abundant, and in terms of gain per effort a successful capture is most likely if preferences are for such a prey. A preference for small prey allows more to be consumed per meal (Table 7.2), and this diminishes the difference in flesh consumption per meal between different prey species. Less energy is expended in catching many, closely-spaced small prey than in searching for and catching a spatially less predictable, albeit larger and richer food source. Robilliard (1971) concluded that asteroids able to catch large, randomly occuring motile prey such as crabs or fish with their pedicellariae had a selective advantage. The use of pedicellariae in prey capture does not interfere with normal feeding activity, and crabs or fish represent a large net energy yield. Crabs and fish accounted for 4.6% of prey items in *A. scabra*, but I was unable to demonstrate that pedicellariae play a role in food capture in this species, but it is nevertheless possible that these structures are involved. Motile organisms can fall prey by coming to rest against the asteroid's tube feet (Young, 1926). The asteroid *Stylasterias forreri* commonly eats motile prey (Robilliard, 1971), and its pedicellariae are functionally adapted for prey capture (Chia and Amerongen, 1975). *Anseropoda placenta* eats only active prey (Hunt, 1925; Clark, 1962) and *Stegnaster inflatus*, which preferentially consumes the anomuran, *Petrolisthes elongatus* has a feeding technique ideally suited to the capture of motile organisms (Grace, 1974). When foraging, *A. scabra* raises the tips of its leading rays (Chapter 4) in a manner similar to that described by Dayton *et al.* (1977) in

Meyenaster gelatinosus and Mauzey *et al.* (1968) for *Solaster dawsoni*. In laboratory aquaria, fish and crabs appeared to be insensitive to the presence of *A. scabra*, and this mode of locomotion may enable tube feet to secure motile prey.

The allocation of prey resources between size classes of *A. scabra* according to a combination of species and size (Figs 7.5, 7.7, 7.8) (Table 7.1), reduces potential intraspecific competition which, if severe enough to limit the consumption of food by individuals, would promote higher predator densities, faster growth, and earlier reproduction (Menge, 1972b). It is noteworthy that intraspecific agonistic behaviour noted by Wobber (1975) in a number of seastar species was never observed in *A. scabra* at Kaikoura.

Food generalisation can be viewed as a strategy which prevents overexploitation of a single food source. *I. maorianus*, *O. neglectus*, *A. glaucus*, *M. aethiops*, *T. smaragdus*, *M. dilatatus*, *E. obtusum* and *R. varia* (8 of the 9 major prey species) have spatial refuges above the foraging range of *A. scabra* (Figs 7.16, 7.17, 7.18). In the case of the first five, this includes both juveniles and adults. Some prey, because of size or escape reactions, are available only to certain seastar size classes. There are extensive areas in the Kaikoura region which although richly populated by the major prey species, contain few or no specimens of *A. scabra*. Prey organisms at these sites could repopulate localities where mortality from predation occurs, so on a regional basis overexploitation by starfish cannot occur. Hilborn (1975) concluded that stability in prey-predator systems depended primarily on dispersal processes.

A. scabra is probably not a keystone species - "the patterns of species occurrence, distribution, and density are disproportionately affected by the activities of a single species of high trophic status" (Paine, 1969b). *P. ochraceous* assumes this role in exposed positions

on the north-west Pacific seaboard by preventing the monopolisation of space by mussels. There does not appear to be a species at Kaikoura within the foraging range of *A. scabra* capable of monopolising food or space, and therefore community organisation in exposed semi-stable boulder habitats in this region is more likely to be structured by competitive interactions between primary consumers.

SUMMARY

1. Only two members of the genus *Astrostole* are now known to be endemic to single island outposts, although all members of the genus are stenobathic.

2. New distribution records show that three of the four south-west Pacific species have relatively wide geographical ranges. This expansion of known ranges is considered to have occurred recently. The dispersal mechanisms involved remain obscure.

3. *A. scabra* is eurytopic and is widespread in New Zealand waters.

4. West Wind Drift is considered to have played only a minor role in the dispersal of the genus. It may have been responsible for the expansion in range of one "cold water" representative. This current system cannot be invoked as the dispersal agent for this essentially sub-tropical genus.

5. The interaction between a west to east current north of the sub-tropical convergence, an eastern Pacific surface gyre, and the Peru Coastal Current, is suggested as a more rational explanation of the distribution of the genus.

6. Intertidal *A. scabra* are moderately mobile, displayed little site specificity, and usually remained within single intertidal pools for less than thirty days. No seasonal vertical migration or intermixing of sub-populations occurred.

7. At Kaikoura, intertidal *A. scabra* are characteristically small ($R \leq 110mm$), sexually immature, are damaged more frequently than subtidal seastars, and do not venture beyond depths of 20m.

Seastars taken from depths of 20-146m are large ($R \geq 110mm$), sexually mature, have thinner skeletons, and are less liable to damage.

8. Longevity in *A. scabra* probably exceeds 6 years and the onset of sexual maturity occurs during the fourth year of life. This is coincident with the adoption of an exclusively subtidal (20-146m) habitat, the attainment of a radius of at least 110mm, and a reduction in skeleton thickness.

9. In 1975, 1976 and 1977, spawning occurred in late August - early September. Gametogenesis commenced in February-March, and gonad index cycles were similar in both males and females. There was no seasonal correlation between gonad and pyloric caeca indices. Gonad volume was also independent of pyloric caeca volume in individual seastars.

10. Only *A. scabra* of $R \geq 110mm$ produced gonads. In intact, subtidal seastars of both sexes, gonad production was dependent on body size such that the volume of gonad produced by August increased linearly with respect to body size. Regeneration partly suppressed gonad production, and large intertidal seastars had reduced gonad indices. The periodicity of reproductive events could not be correlated unequivocably with any physical or biotic exogenous environmental factor.

11. Dietary composition in *A. scabra* was ascertained by regular sampling of four, geographically separated, intertidal sub-populations between January 1976 and January 1977. The species is a food generalist and scavenger with a diet composed chiefly of molluscs and crustaceans belonging to more

than sixty genera. The diet was dominated numerically by chitons and trochid molluscs. Several site-specific differences in dietary composition were apparent. Only *Ischnochiton maorianus* was a numerically important prey species at each site. Despite differing diets at each site, dietary diversity and evenness were maintained at comparable levels.

12. The proportion of intertidal seastars feeding fluctuated seasonally during one year of study, and reached a peak of 42% in January and fell to 23.7% in June 1976. The diet remained generalised throughout the year and no single prey species was subjected to seasonally variable predation pressure. Prey species were eaten in proportions independent of their abundance.

13. In laboratory aquaria, *A. scabra* free of ingestive conditioning could discriminate between different prey species and preferentially consumed *I. maorianus*. A rank order of preference was established for five numerically important prey species. Strong prey preferences existed at the specific, but not at the familial level.

14. Sixteen molluscs and one echinoid exhibited reactions to contact with *A. scabra*. Two abalone, *Haliotis iris* and *H. australis*, were able to discriminate between foraging and non-foraging *A. scabra*.

15. Dietary composition altered qualitatively with increased seastar size and five, size-dependent shifts in dietary composition were isolated. However, seastars in different size classes had diets which overlapped broadly with respect to prey species. There

was little dietary overlap between seastar size classes on the basis of prey size.

16. Eight of nine major prey species have spatial and size refuges from predation by *A. scabra*. Size-discriminant predation was detected in wild, intertidal *A. scabra* so that large *Turbo smaragdus*, *Risellopsis varia*, small *Melagraphia aethiops*, and intermediate sized *Micrelenchus dilatatus*, *I. maorianus*, *Onithochiton neglectus* and *Amaurochiton glaucus* were consumed at levels disproportionate to their abundance in the habitat.

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